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Seasonal migration and distribution of female red king crabs in a southeast Alaska estuary

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SEASONAL MIGRATION AND DISTRIBUTION OF FEMALE RED KING CRABS IN A SOUTHEAST ALASKA ESTUARY

A

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SEASONAL MIGRATION AND DISTRIBUTION OF FEMALE RED KING CRABS IN A SOUTHEAST ALASKA ESTUARY

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Abstract

Seasonal movements and distribution of primiparous and multiparous red king crabs (*Paralithodes camtschaticus*) were monitored approximately weekly for one year in Auke Bay, Alaska, using ultrasonic biotelemetry. Patterns of seasonal movements were generally similar for all crabs, although movements of multiparous crabs were more conservative and coordinated between individuals. Groups of crabs remained in relatively discrete areas for several weeks before moving, usually as a group, to a different area. The annual range of primiparous crabs ($\bar{x}$ = 11.9 km^2) exceeded ($P < 0.025$) that of multiparous crabs ($\bar{x}$ = 3.6 km^2). All crabs displayed distinct seasonal shifts in depth distribution and habitat use. Depth distribution was significantly correlated with photoperiod and the abrupt, synchronous movement of crabs between habitats was coincident with thermohaline mixing. Females displayed a highly aggregated distribution, especially during winter in shallowwater areas. Podding behavior of adult crabs was documented for the first time. Possible causes and functions of this highly specialized behavior are discussed.

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CHAPTER I.

MIGRATION OF MARINE CRUSTACEA

Many marine crustaceans undertake temporally organized and spatially oriented movements, which facilitate basic biological functions, such as feeding, growth and reproduction (Allen, 1966). In addition, most crustaceans exhibit consistent daily locomotor activities, including feeding excursions, exploratory movements, courtship behavior and escape reactions (Creutzberg, 1975). Bainbridge (1961) suggested that migrations could be interpreted as valuable adaptations placing the animal under conditions more suitable for a particular life history stage or physiological state. Certainly, many movements involve habitat selection, whereby the animal maintains or seeks a particular environment with optimal physical, chemical and biological conditions promoting maximum survival (Creutzberg, 1975).

How do crustaceans maintain proper orientation with respect to their surroundings and to what stimuli do they respond during migratory movements? Creutzberg (1975) pointed out that the particular condition searched for during migratory movements might not necessarily be the factor to which an animal responds for orientation. Harden-Jones (1980) differentiated between two types of available information: clues and cues. Migrants rely on clues while en route and ultimately use them to recognize or identify a particular habitat upon arrival.

Cues are the means by which behavior and migratory movements are integrated in time with temporal changes in the environment. In short, clues provide information as to "where" and cues provide information as to "when."

Benthic and pelagic movements of crustaceans generally are not random, but are highly organized with respect to their environments (Allen, 1966). Movement patterns and habitat types occupied by marine crustaceans are diverse and probably require the employment of an equally diverse range of orientational and navigational mechanisms. The objective of this chapter is to identify commonly employed orientational mechanisms and to illustrate the adaptive variability of several disparate taxa of marine crustaceans.

The diurnal vertical migration of copepods has been described as the most spectacular of pelagic migrations (Bainbridge, 1961). Vertical movements of planktonic crustaceans, which also include cladocerans, mysids, isopods, amphipods, euphausiids, and decapods, may extend over several hundred meters. Diurnal vertical migration may have several selective advantages. Upward migration is essentially a feeding response, while downward migration has variously been reported as an escape from the harmful effects of sunlight, toxic products of phytoplankton, and predators adept at detecting prey in sunlight (Bainbridge, 1961). Zooplankton may also derive metabolic benefits from these migrations (McLaren, 1963). The energetic losses of vertical migration are offset by: 1) an increased rate of food assimilation during nocturnal foraging in warmer

waters; and 2) a decreased metabolism at cooler, daytime depths (McLaren, 1963).

Light is thought to be the dominant environmental factor controlling diurnal vertical migrations (Forward, 1976), and may also serve as an initiating and/or an orientating cue for these movements (Bainbridge, 1961). Rose (1925) proposed that light alone could be the controlling mechanism if the animals select a zone of optimum light intensity or isolume. Forward (1976) suggests, however, that the rate and duration of change in light intensity from the ambient or adaptation intensity might serve as the cue for initiating vertical movements. Endogenous timing processes probably also play a significant role in these movements (Enright and Hamner, 1967). The effects of temperature and the thermocline (Cushing, 1951), salinity (Banse, 1964), pressure (Rice, 1964) and gravity (Hardy and Paton, 1947) have also been reported, or suggested, to affect vertical zooplankton migrations.

The vertical migration of crustacean zooplankton might be influenced by the physical effects of phytoplankton, including reductions of light intensity and secretion of repellent or attractive products (Bainbridge, 1961). Dingle (1962) demonstrated an interesting correlation between different wavelengths of light and movement of several planktonic crustacea. Movements of some anomuran and brachyuran larvae in blue light have a strong horizontal component producing extensive wandering, while red light predominately induces a vertical hop and sink behavior interpreted as a station-keeping mechanism. Since algae filter out blue

light, larvae will tend to be concentrated in areas of dense phytoplankton. Location of food is believed to be the functional significance of these behavioral responses in *Daphnia* (Smith and Baylor, 1953). Fish predation can directly induce diel vertical migration of the planktonic copepod, *Acartia hudsonica* (Bollens and Frost, 1989). Apparently, this response is not due to chemical exudates from the fish, but possibly to visual or mechanical stimuli.

Horizontal pelagic migrations have not been well studied, but have been observed in a few species of mysids, euphausiids, and natant decapods (Bainbridge, 1961). Both daily and seasonal migrations have been described, and have been associated with ontogenetic shifts in habitat use, feeding and spawning. The onshore-offshore seasonal migrations of the shrimp, *Crangon crangon*, are thought to be initiated by the reversal of temperature differences between inshore and offshore waters (Hartsuyker, 1966). This species also undertakes daily feeding migrations onto the tide flats, which are thought to be initiated by tidal movements (Hartsuyker, 1966). The offshore escape response of the shrimp, *Palaemonetes vulgaris*, is mediated by sun compass orientation, and possibly by underwater polarized light patterns (Goddard and Forward, 1989).

Inhabitants of sand beaches and other shoreline communities have several behavioral strategies to find and remain in optimal habitat. They often employ a diverse suite of environmental cues for orientation, depending on their availability. The homing behavior of talitrid amphipods provides a well-illustrated

example of this ability. *Orchestoidea* is known to utilize time-compensated celestial orientation, but may also use backshore landmarks, substrate characteristics (degree of slope, moisture, and texture), and wind direction as cues during homing migrations (Enright, 1978). Locomotor activity of *Traskorchestia traskiana* is partly controlled by endogenous circadian rhythms, and is synchronized and maintained by fluctuating light intensity (Koch, 1989). This supralittoral beach-hopper also performs an escape response up the beach during tidal inundation (Koch, 1989). In addition to orientating with a time-compensated celestial compass, *Talitrus* and *Talorchestia* are thought to utilize polarized skylight, the magnetic field, and sky color differences over land and sea (Pardi and Ercolini, 1986).

Other beach-dwelling crustaceans which rely on celestial cues and gross landmarks for orientation include the sand fiddler crab, *Uca pugilator* (Herrnkind, 1968). Celestial navigation by tylid isopods is thought to be guided by the sun, polarized light, or the moon (Hamner *et al.*, 1968). Directional decisions made by the burrowing crab *Emerita* and the amphipod *Synchelidium* are apparently independent of visual cues. These crustaceans respond to acute changes in hydrostatic pressure associated with wave movement, and *Synchelidium*, at least, relies on critically-timed reversals of phototaxis during tidal migrations (Enright, 1978).

Benthic migrations of intertidal and subtidal crustaceans are common and generally involve seasonal inshore/offshore movements associated with physiological changes (Bainbridge, 1961; Allen, 1966). These animals occupy habitats with different environmental conditions than beach inhabitants and naturally utilize several distinct orientational guideposts.

The autumnal mass migrations of the palinurids have been well documented, probably due to their widespread commercial importance (Herrnkind, 1980). Kanciruk and Herrnkind (1978) circumstantially implicate storm-induced declines in water temperature as the triggering stimulus of mass migrations of *Panulirus argus* at Bimini, Bahamas. Whether rapid temperature declines or a threshold temperature serve as the migratory cue is unclear. The migratory population inhabits shallow water where these autumnal storms have a profound effect. The orientational mechanisms responsible for the strong directionality of these migrations are poorly understood, although both water currents and water oscillations near bottom from surge and swell can act as guideposts (Herrnkind and McLean, 1971). Although this species does have vernal reproductive movements, the offshore mass migrations observed during autumn are apparently independent of reproduction (Kanciruk and Herrnkind, 1976), and might be an adaptation to avoid severe winter conditions in shallow water areas (Herrnkind, 1980).

The onset and duration of nocturnal locomotor activity changes seasonally in *Panulirus argus*, and might be in response to changes in photoperiod (Kanciruk and Herrnkind, 1978). Decreases in photoperiod preceeding the autumnal mass migration induces the onset of Zugunruhe, or hyperactivity (Herrnkind and Kanciruk, 1978). Short-term foraging migrations of juvenile western rock lobsters, *Panulirus cygnus*, and the Norway lobster, *Nephrops norvegicus*, are initiated by changes in light intensity (Chapman *et al.*, 1975; Jernakoff, 1987).

Seasonal variations in water temperature are thought to influence the seasonal onshore/offshore migrations of several other subtidal decapods, including *Panulirus interruptus* (Mitchell *et al.*, 1969), *Carcinus maenas* (Atkinson and Parsons, 1973), *Pagurus longicarpus* (Rebach, 1974), and *Callinectes sapidus* (Warner, 1976). The blue crab, *Callinectes sapidus*, also conceivably uses celestial orientation during intertidal movements and when swimming near the surface during long-distance migrations (Nishimoto and Herrnkind, 1982). Wave surge has been identified as an important orientational clue during the seasonal migration of *Limulus* (Ireland and Barlow, 1978). *Cancer pagurus* and *Homarus americanus* females undertake seasonal breeding migrations, but the underlying migratory mechanisms are unclear (Saila and Flowers, 1968; Bennett and Brown, 1983; Campbell and Stasko, 1985).

Female Dungeness crabs, *Cancer magister*, display a seasonal movement pattern consisting of a spring inshore movement and a fall offshore movement in

northern California. Diamond and Hankin (1985) suggested that these movements are closely associated with the reproductive cycle. Smith and Jamieson (1991) reported that Dungeness crabs might move in response to environmental clues such as tides and currents. This apparent relationship between direction of movement and prevailing currents was also noted for male Dungeness crabs (Gotshall, 1978). The red king crab, *Paralithodes camtschaticus*, also undertakes seasonal migrations associated with the reproductive cycle, but the proximate factors involved in these movements are poorly understood.

Migration is a highly specialized behavior which permits adaptation to changing environments. Orientational and navigational mechanisms employed by crustaceans are as diverse as the habitats they occupy. Crustaceans with wide-ranging movements must be capable of utilizing orientation cues perceivable in highly varied conditions (Nishimoto and Herrnkind, 1982). In many cases migration involves a hierarchy of cues, although the basis for choice or detection of certain cues remains somewhat obscure (Dingle and Gauthreaux, 1991). Herrnkind (1968) emphasized the adaptive value of the ability of some animals to modify their responsiveness to different cues under certain conditions. The use of multiple clues is probably an adaptive response, since no single clue provides adequate directional information under all conditions.

CHAPTER II.

SEASONAL MIGRATION OF FEMALE RED KING CRABS IN AUKE BAY, ALASKA

Introduction

Seasonal migration of red king crab, *Paralithodes camtschaticus* (Tilesius), has been the subject of several investigations since commercial harvest of the species began in the early 1900's. The majority of these investigations have centered on the historically important commercial areas of the eastern Bering Sea, Bristol Bay, Kodiak Island and Cook Inlet (Bright *et al.*, 1960; Hayes and Montgomery, 1962; Powell and Reynolds, 1965; Simpson and Shippen, 1968).

Several studies on migratory movement have also been conducted along the west coast of Kamchatka, where the Japanese and Russian fleets have historically harvested king crabs (Rumyantsev, 1945; Yamamoto, 1961). These studies focused primarily on males. Powell (1965) and Bright (1967) tagged both males and females, but because the tags were recovered by the commercial fleet, sampling effort was concentrated in those areas yielding the most legal males. Because these areas did not necessarily coincide with areas of high female abundance, sampling effort was biased toward males and consequently, data on female movements remain limited.

Although many aspects of their migratory patterns are still unclear, it is widely accepted that in the late winter and early spring mature male and female red king crabs begin to appear in large aggregations in nearshore shallow waters. The time of appearance of the two sexes in nearshore waters, however, is not synchronous, with the males arriving first. Males generally molt enroute to the shallows. Bright (1967) conjectured that eggs attached to the females' pleopods hatch during migration to shallow water (Bright, 1967), after which courting, molting and mating occur. Following a period of from two to four months (Bright, 1967; personal observations) when both males and females occur in shallowwater areas, the two sexes undertake independent migrations to deeper water. Bright (1967) suggested that adults occur in discrete groups, separated by age and sex, during different phases of the annual migration. Movement from deep to shallow water has been referred to as the "spawning migration", and the subsequent migration to deeper water as the "feeding migration" (Bright 1967).

Female red king crabs are thought to become sexually mature at five and one-half years of age (Bright *et al.*, 1960). Size at maturity varies markedly at different locations, ranging from 75 to 113 mm carapace length (CL) (Vinogradov, 1945; Gray, 1963). The smallest ovigerous female red king crab caught in pot surveys conducted in Auke Bay during March-May 1988 was 93 mm CL (unpublished data). Females are termed primiparous during their initial year of maturity and generally produce fewer eggs than multiparous females (those that

have reproduced at least once previously). Hsu (1987), however, concluded from his analysis of National Marine Fisheries Service trawl survey data that in some years primiparous females may comprise up to 99% of the total reproductive stock in the eastern Bering Sea, and may therefore significantly contribute to the annual reproductive effort.

Female red king crab display strongly synchronized seasonal reproduction (Sloan, 1985; Shirley and Shirley, 1989), however, recent laboratory studies suggest that the precise timing of events related to reproduction varies with female body size. These studies have shown a significant direct relationship between female carapace length and time of larval hatch and ecdysis (Shirley and Shirley, 1988b; Carls and O'Clair, 1990). The laboratory results are supported by field observations of primiparous females being courted in shallow water a month or more before multiparous females (Powell *et al.*, 1972; personal observations). A bimodal density pattern of red king crab larvae (zoeae I) was evident in plankton samples collected from Auke Bay during the period 1985-89, implying that larvae had hatched during two distinct time periods (Shirley and Shirley, 1989; Shirley and Shirley, 1990). These observations suggest that primiparous individuals may begin egg incubation and depart shallow water for the deeper feeding grounds before multiparous crabs. If such a temporal shift in the initiation of migration from the shallow water grounds occurs, the patterns of movement of the two groups may differ. The relative timing of larval hatch between the two groups

may be influenced by differences in timing of egg extrusion and patterns of movement and depth distribution the following year.

Bainbridge (1961) suggested that the variables initiating migrations of crustaceans are primarily physiological and in direct response to the biological needs of breeding, molting and feeding. The factors that trigger the annual migration of red king crab are unknown. Bright (1967) conjectured that the proximate cause of these movements was some unspecified environmental cue. Ultimately, movements may be controlled by the availability and abundance of food, seasonal differences in water temperature (Rumyantsev, 1945; Rodin, 1970) or other abiotic factors such as photoperiod.

The goal of this study was to provide a detailed view of the annual migration of females in one population of red king crabs with emphasis on the differences that may exist between primiparous and multiparous individuals, and to relate these movements to seasonal changes in environmental factors such as water temperature, salinity, and photoperiod.

Materials and Methods

This study was conducted in Auke Bay, Alaska (Figure 1), which has a water surface area of about 13 km^2 at MHHW. Approximately 45% of the bay is between 40 and 60 m in depth (Figure 1). Temperatures and salinities in this depth range vary annually from 2° to 7.8°C and between 29.5‰ and 32‰, respectively (Bruce *et al.* 1977).

Primiparous females (CL < 108 mm, $\bar{x}$ = 102.8 mm) were collected with baited pots from two areas of Auke Bay, and multiparous females (CL > 124 mm, $\bar{x}$ = 149.4 mm) were collected by divers near the head of the bay (Figure 1). Because areas where both size classes co-occurred could not be found, primiparous and multiparous crabs were collected from different locations. All crabs were transported to the Auke Bay Laboratory where carapace length and wet weight were recorded (Table 1).

Ultrasonic tags with a two-year life expectancy were attached to ten crabs from each size class. Only ovigerous females in good physical condition were tagged. Each transmitter (Sonotronics model CHP-87) had a unique aural code and a range of about 2 kilometers. The tags were 105 mm in length and 16 mm in diameter and weighed approximately 13 grams in water (less than 2% of the total body weight for primiparous crabs and less than 1% for multiparous crabs).

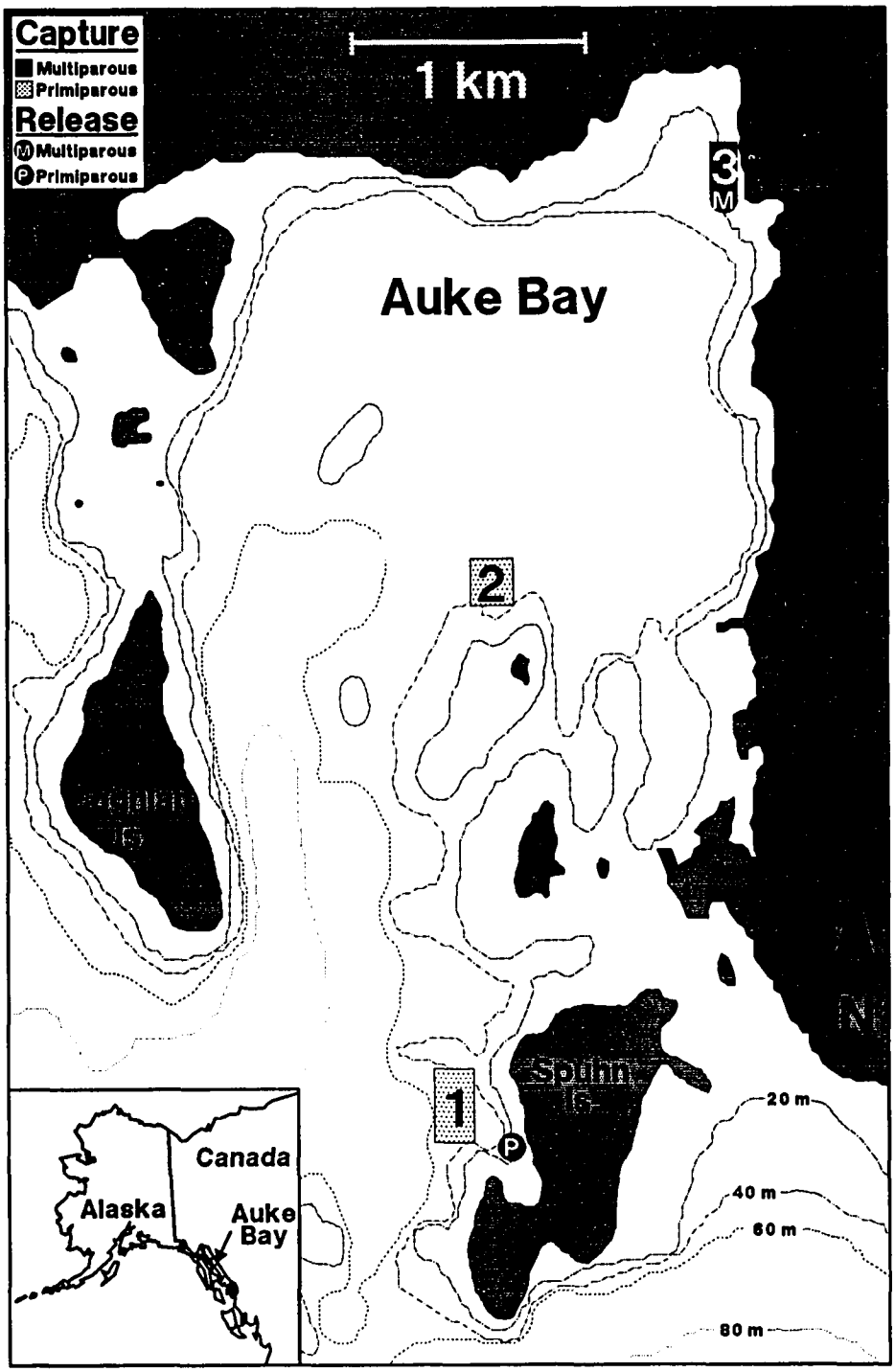


Figure 1. Study area at Auke Bay, Alaska showing areas where female red king crabs fitted with ultrasonic transmitters were caught and released. Depth contours are in meters. UAF = University of Alaska Fairbanks. Numbers refer to capture sites (see Table 1).

Table 1. Tag number, carapace length, wet weight, capture site, and date of capture for 22 female red king crabs fitted with ultrasonic transmitters.

Tag No.	Carapace Length (mm)	Wet Weight (g)	*Capture Site	Date of Capture
Primiparous Females				
249	103.8	819.2	1	5/04/88
267	98.1	687.2	1	4/19/88
339	104.5	827.8	1	4/29/88
339A	106.1	926.6	1	7/22/88
348	102.2	811.8	1	4/26/88
357	102.8	852.6	1	4/26/88
366	93.6	637.7	2	5/04/88
375	108.0	980.8	2	5/04/88
384	105.1	855.7	2	5/04/88
447	103.2	816.3	1	4/26/88
456	106.4	925.7	2	5/04/88
Multiparous Females				
2228	154.3	2240.8	3	5/06/88
2237	167.1	2783.7	3	5/10/88
2246	141.8	1759.1	3	5/06/88
2255	156.0	2453.4	3	5/10/88
258	124.5	1516.6	3	5/06/88
276	152.0	2224.1	3	5/05/88
285	146.4	1905.6	3	5/06/88
294	148.4	1936.6	3	5/10/88
465	150.8	2118.2	3	5/06/88
465A	162.3	2763.5	1	7/22/88
555	153.0	2192.0	3	5/06/88

* Refer to figure 1 for location of capture sites.

The tags were directly attached to the carapaces of primiparous females with non-toxic SeaGoin' Poxy Quik 5-minute epoxy putty in the groove between the gastric and cardiac regions. The carapaces of the multiparous crabs were still in the final stages of hardening following ecdysis; consequently the epoxy did not adhere to these carapaces as well as to the carapaces of the primiparous individuals. Therefore, the tags were attached to these crabs with plastic cable ties wrapped around the carapace between the first and second walking legs. I conducted a laboratory experiment to determine if the tagging methods used in this study modified crab behavior. Twenty-four crabs (12 primiparous and 12 multiparous) were randomly assigned to three treatments (eight crabs per treatment) as follows: 1) tags attached with epoxy putty, 2) tags attached with plastic cable ties, and 3) controls with no tags. Two independent tests were conducted for 20 days: 1) each day, an equal portion of blue mussels (*Mytilus trossulus*) were presented to each crab, and the following day the percentage of mussels consumed was recorded, and 2) the time required for a crab to right itself when overturned under water was recorded daily. Neither tagging treatment significantly ($P > 0.05$; F-Test) affected food consumption by the crabs. Similarly, neither tagging method significantly ($P > 0.25$; F-Test) affected the righting response of the crabs.

Both groups of crabs were released near the site of capture (Figure 1) to minimize disorientation of the crabs associated with release in an unfamiliar area

(Powell, 1964). To minimize stress and injury to the crabs, they were lowered to the bottom in a modified king crab pot and set free by divers. Primiparous and multiparous crabs were released on 17 May and 3 June, respectively.

The positions of the crabs were usually fixed weekly (Table 2), as weather permitted, with an ultrasonic receiver (Sonotronics model USR-4D) and directional hydrophone (Sonotronics model DH-2) with a beam width of ±6 degrees at half-power points. A small float was deployed after the boat was positioned over a crab. The boat was maintained at this float while its position was fixed by measuring angles between three shoreward markers with a beam-converging sextant (O'Clair *et al.*, 1990). I estimated the error associated with this "mark on top" method to be ±30.3 m. This value was obtained by calculating the mean distance between fixes for those tags that were considered stationary and no longer on live crabs.

Depth was measured with a Hummingbird Model 4080D depth finder, and is reported in meters relative to mean lower low water (MLLW). Near-bottom water samples in the vicinity of individual crabs or groups of crabs were collected during each tracking period with a Niskin bottle equipped with reversing thermometers. The salinity of these samples was measured in the laboratory with a Beckman bench salinometer. During the last six-month period of this study water column profiles of temperature and salinity were obtained with a Seabird Electronics Seacat Profiler at nine stations throughout the study area (Niskin

Table 2. Week number, dates (inclusive) and number of female red king crabs tracked during each week of the 1988-89 study period.

Week No.	Dates	No. of Crabs	Week No.	Dates	No. of Crabs
1	5/16-5/22	10	29	11/28-12/01	16
2	5/23-5/29	9	30	12/05-12/11	0
3	5/30-6/05	19	31	12/12-12/18	15
4	6/06-6/12	0	32	12/19-12/25	0
5	6/13-6/19	7	33	12/26-1/01	0
6	6/20-6/26	15	34	1/02-1/08	15
7	6/27-7/03	16	35	1/09-1/15	12
8	7/04-7/10	16	36	1/16-1/22	0
9	7/11-7/17	15	37	1/23-1/29	5
10	7/18-7/24	8	38	1/30-2/05	0
11	7/25-7/31	15	39	2/06-2/12	16
12	8/01-8/07	18	40	2/13-2/19	0
13	8/08-8/14	17	41	2/20-2/26	15
14	8/15-8/21	18	42	2/27-3/05	0
15	8/22-8/28	18	43	3/06-3/12	12
16	8/29-9/04	18	44	3/13-3/19	15
17	9/05-9/11	17	45	3/20-3/26	0
18	9/12-9/18	17	46	3/27-4/02	13
19	9/19-9/25	17	47	4/03-4/09	13
20	9/26-10/02	16	48	4/10-4/16	13
21	10/03-10/09	17	49	4/17-4/23	12
22	10/10-10/16	17	50	4/24-4/30	9
23	10/17-10/23	17	51	5/01-5/07	10
24	10/24-10/30	16	52	5/08-5/14	9
25	10/31-11/06	16	53	5/15-5/21	6
26	11/07-11/13	16	54	5/22-5/28	3
27	11/14-11/20	16	55	5/29-6/04	1
28	11/21-11/27	0			

bottle sampling was discontinued at this time). Temperature and salinity of depths occupied by crabs were estimated from the profile at the nearest station to each crab. Photoperiod was calculated for each tracking period from a table of local mean time of sunrise and sunset (U.S. Department of Commerce, 1988).

SCUBA was used to make observations of tagged crabs when they were within diving depth (< 35m), and to recover derelict tags (i.e., tags which became detached from crabs) and molting tagged crabs during spring 1989. Divers used a submersible receiver/hydrophone (Sonotronics model USR-88) to locate tags underwater.

Unless otherwise stated, one-way analysis of variance (ANOVA) was used to test for differences between means of variables. All means of time-series variables (i.e., depth, water temperature, salinity and movement rate) are weighted means, and are presented as the mean ± 1 standard error of the mean (SE). The Kruskal-Wallis test was substituted when data failed to meet the assumptions of the ANOVA. All movements were charted with a microcomputer design and drafting program (Autodesk, 1988).

Annual range, or the area within which a crab moved throughout the study period, was estimated by the minimum-convex polygon method (Worton, 1987). Activity rate was calculated as distance moved in meters divided by time in days between successive observations.

Results

The movements of seven primiparous and five multiparous females were monitored through one complete reproductive cycle (11-12 months), and only these crabs were included in the analysis of annual movements. Analysis of seasonal movements included only those crabs that had movement through that entire season (Table 3). Three seasons were delimited for this study based on crab movements and physical oceanographic cycles as follows: 1) a summer/fall period from June through mid-November, when crabs inhabited deep waters ($\overline{x}$ = 52.6 m) below a well developed thermocline; 2) a winter period from mid-November through early March, when crabs inhabited shallow waters ($\overline{x}$ = 27.5 m) and when the water column was well-mixed and essentially homogeneous with respect to temperature and salinity; and 3) a spring period from early March through late May marked first by crab movement to intermediate depths ($\overline{x}$ = 33.5 m) and then by movement into shallow water to molt and mate in April/May. This period was also characterized by the redevelopment of the thermocline and halocline during late March.

Two additional crabs were tagged during the study as derelict tags were recovered by divers (crabs 339 and 465). In addition to the two tags recovered by divers, five tags remained stationary at depth; possibly due to predation, natural mortality or entrapment in derelict crab pots. Observations from a manned

Table 3. Number of female red king crabs tracked completely through each of three seasons delimited for this study.

Season	Primiparous	Multiparous
Summer/Fall	7	7
Winter	8	7
Spring	7	6

submersible confirmed the entrapment of an ultrasonically-tagged red king crab from a concurrent study in Auke Bay. One tag (No. 456) could not be located 16 weeks after release, possibly due to tag malfunction or movement outside of the study area. The remaining tag was received in an anonymous package with a note indicating the crab had been caught in the local sport fishery. Individual tracking records including the fate of each crab are listed in Appendices 1 - 22, and were used to map movements of each crab (appendices 23 - 44). A summary of total days each crab was tracked and total distance moved is presented in Appendix 45.

All crabs in this study followed a general pattern of seasonal movement that can be divided into three phases: 1) gradual movement from shallow to deeper water after mating and egg extrusion, and residence there through early November; 2) abrupt, synchronous movement into shallowwater areas in November, and residence there through late February or early March; and 3) gradual, synchronous movement to intermediate depths followed by movement into shallowwater areas to molt and mate between late March and late May.

During early summer primiparous crabs had moved into the deeper parts of the bay near the Coghlan Island trench (Figure 2). By mid-summer these crabs had split into two main groups. One group of four crabs moved out of the bay into adjacent Stephens Passage and occupied areas deeper than 100 meters by late summer. The other group of four crabs moved into the inner bay and occupied areas adjacent to and often overlapping those occupied by multiparous crabs.

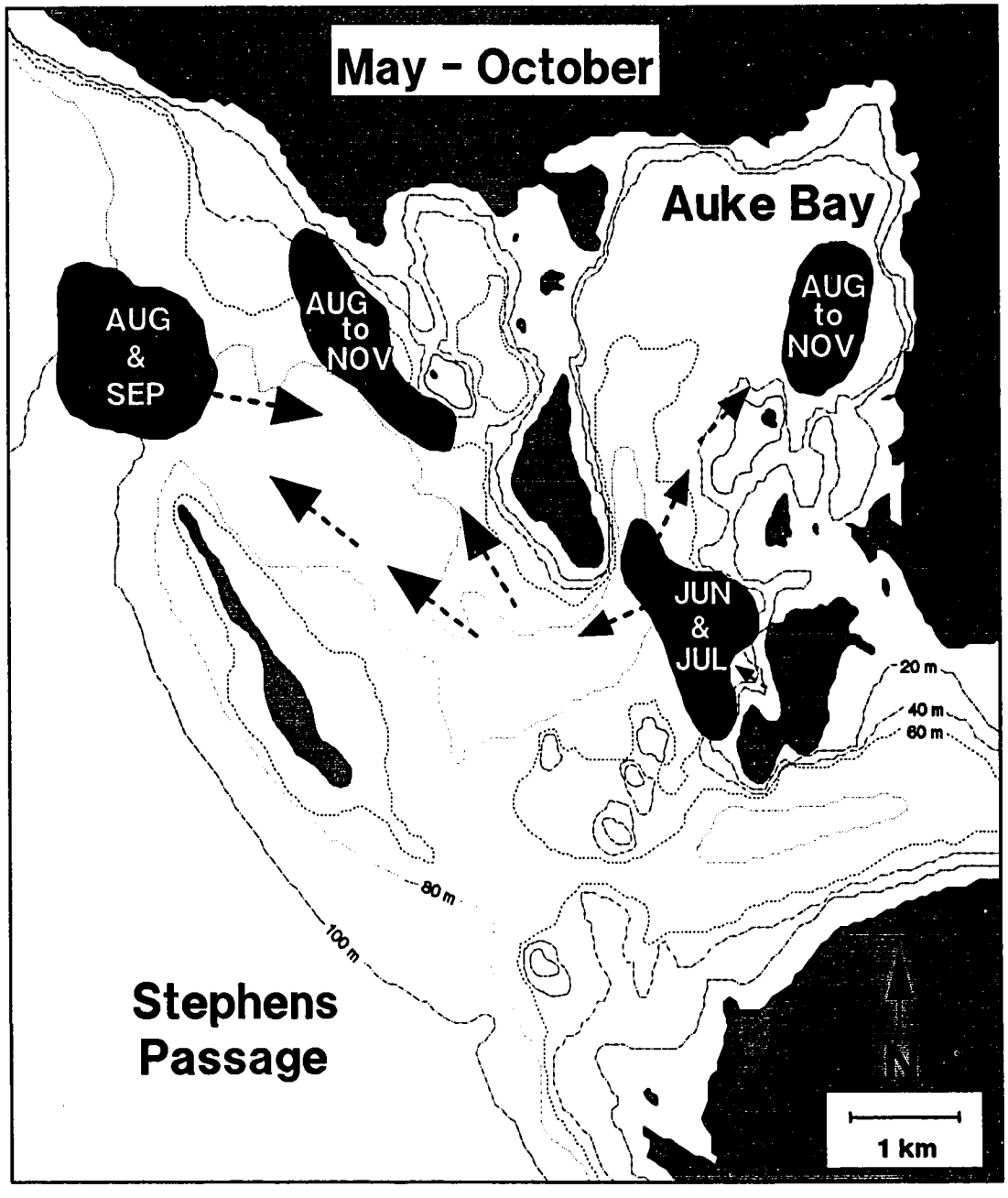


Figure 2. Areas of distribution of primiparous female red king crabs fitted with ultrasonic transmitters from May through October 1988. Arrows indicate large-scale movement of crabs.

Both groups of primiparous crabs remained in deeper water areas through early fall, when they moved into shallowwater areas.

In contrast, multiparous females all remained within inner Auke Bay during the summer/fall period and were generally distributed only along the eastern side of the bay, presumably as a loosely-knit feeding aggregation at depth (Figure 3). These crabs also remained at depth through early fall when they moved into shallowwater areas.

Both primiparous and multiparous females remained in shallowwater areas between November and early February (Figure 4 and Figure 5), and diver observations during this period revealed that these crabs were often in dense aggregations estimated to consist of as many as 300 individuals. These aggregations usually comprised both primiparous and multiparous females, and crabs were observed feeding on shallowwater invertebrates on several occasions. During February both groups of crabs began to move to intermediate depths, although a few individuals remained in isolated aggregations in shallow water.

The movement patterns of primiparous females were varied between March and May (Figure 6). A few primiparous crabs remained in shallow water and made only sporadic movements to deeper water before molting and mating occurred (Figure 6, polygon A). Several primiparous females, however, made extensive migrations to areas previously not occupied by tagged crabs to molt and mate (Figure 6, polygon B). Even the three primiparous females closely

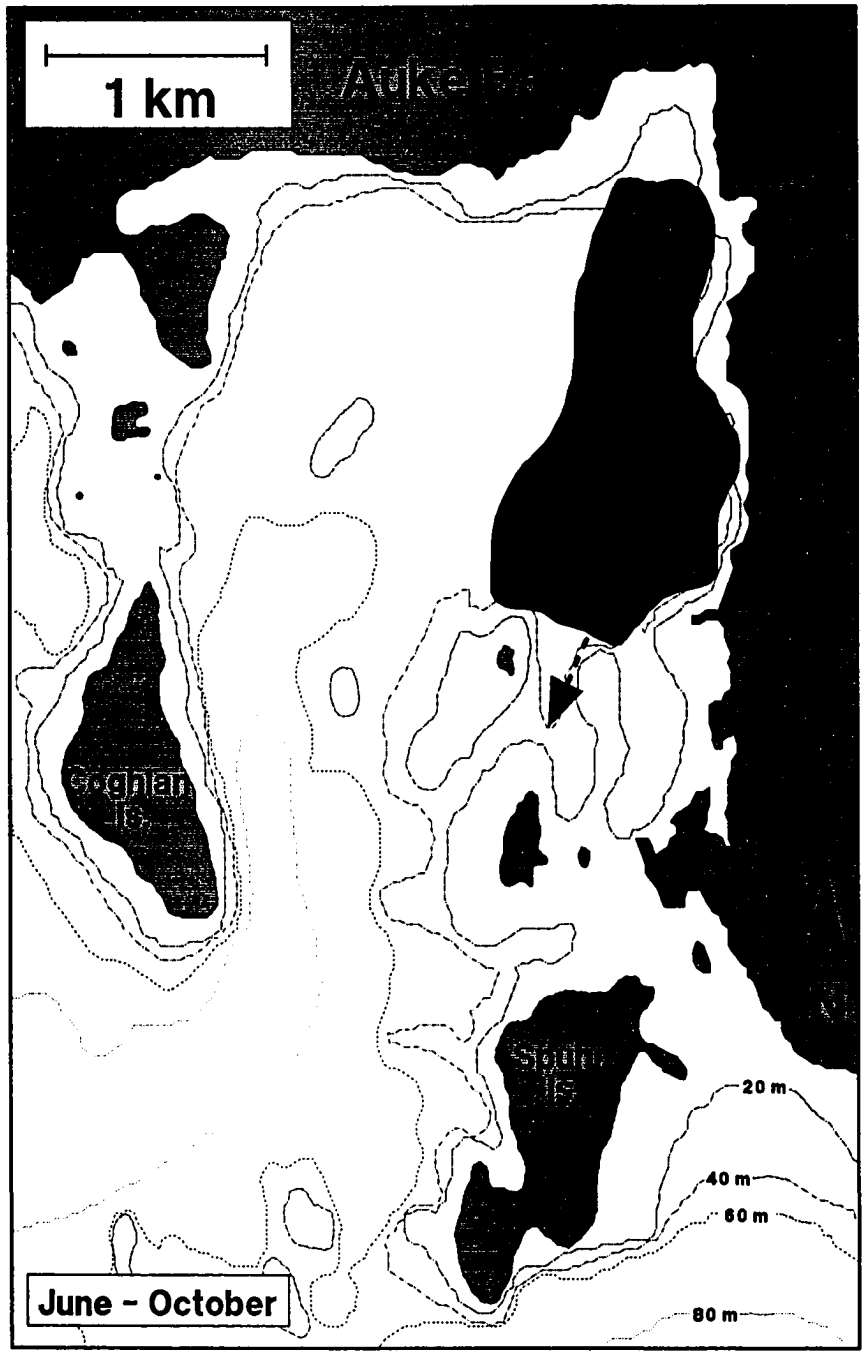


Figure 3. Areas of distribution of multiparous female red king crabs fitted with ultrasonic transmitters from June through October 1988. Arrows indicate large-scale movement of crabs. UAF = University of Alaska Fairbanks.

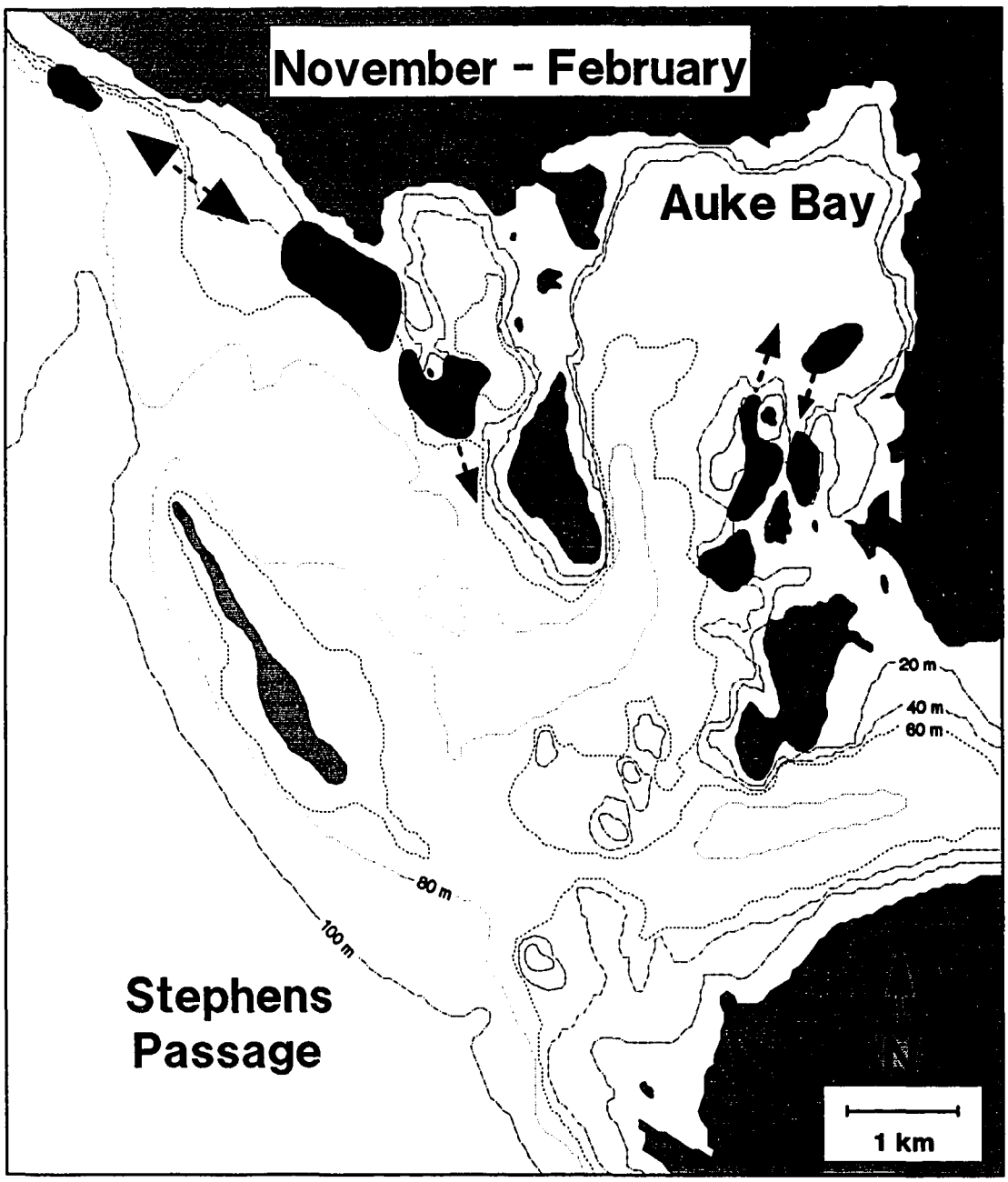


Figure 4. Areas of distribution of primiparous female red king crabs fitted with ultrasonic transmitters from November 1988 through February 1989. Arrows indicate large-scale movement.

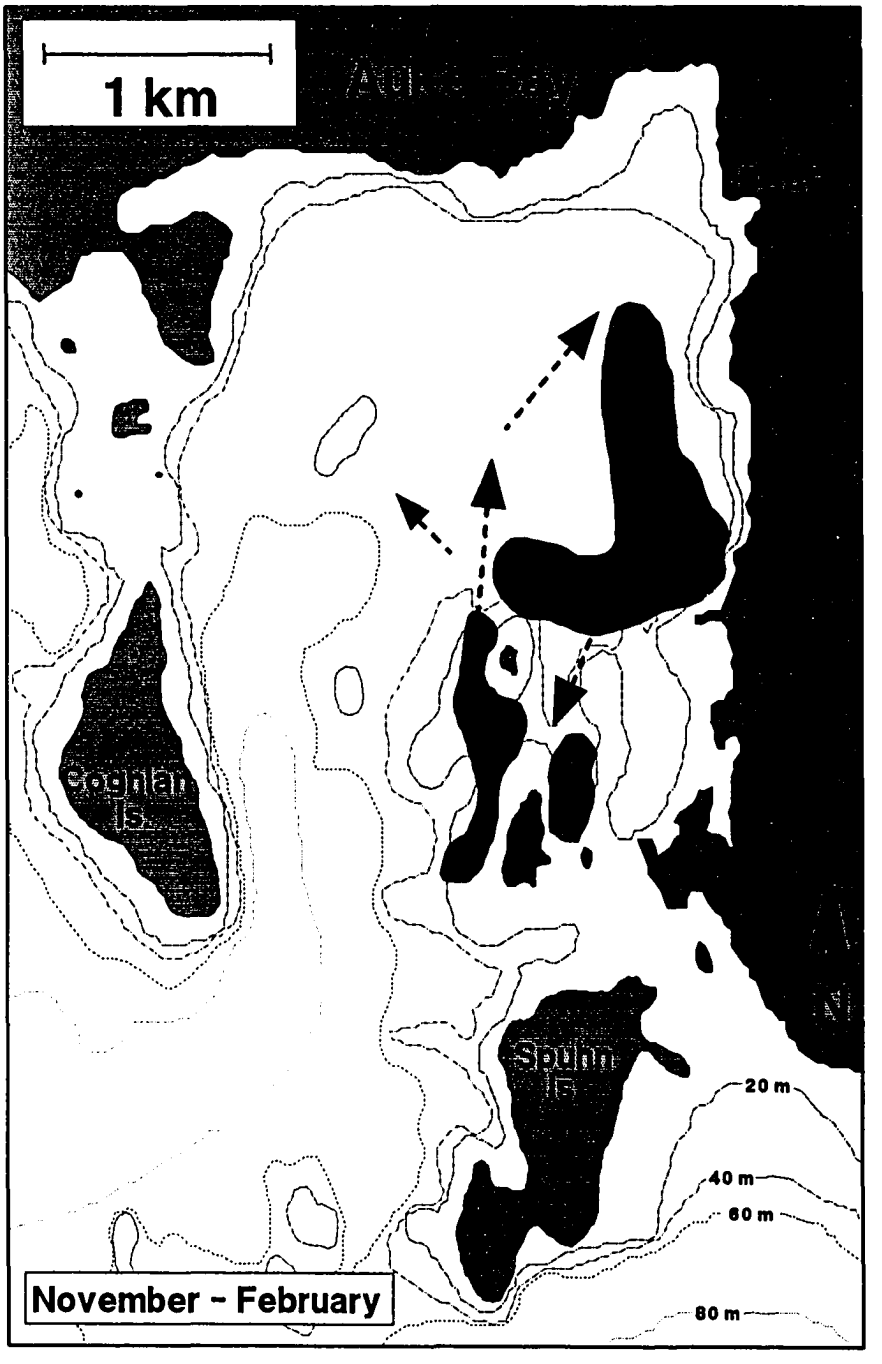


Figure 5. Areas of distribution of multiparous female red king crabs fitted with ultrasonic transmitters from November 1988 through February 1989. Arrows indicate large-scale movement. UAF = University of Alaska Fairbanks.

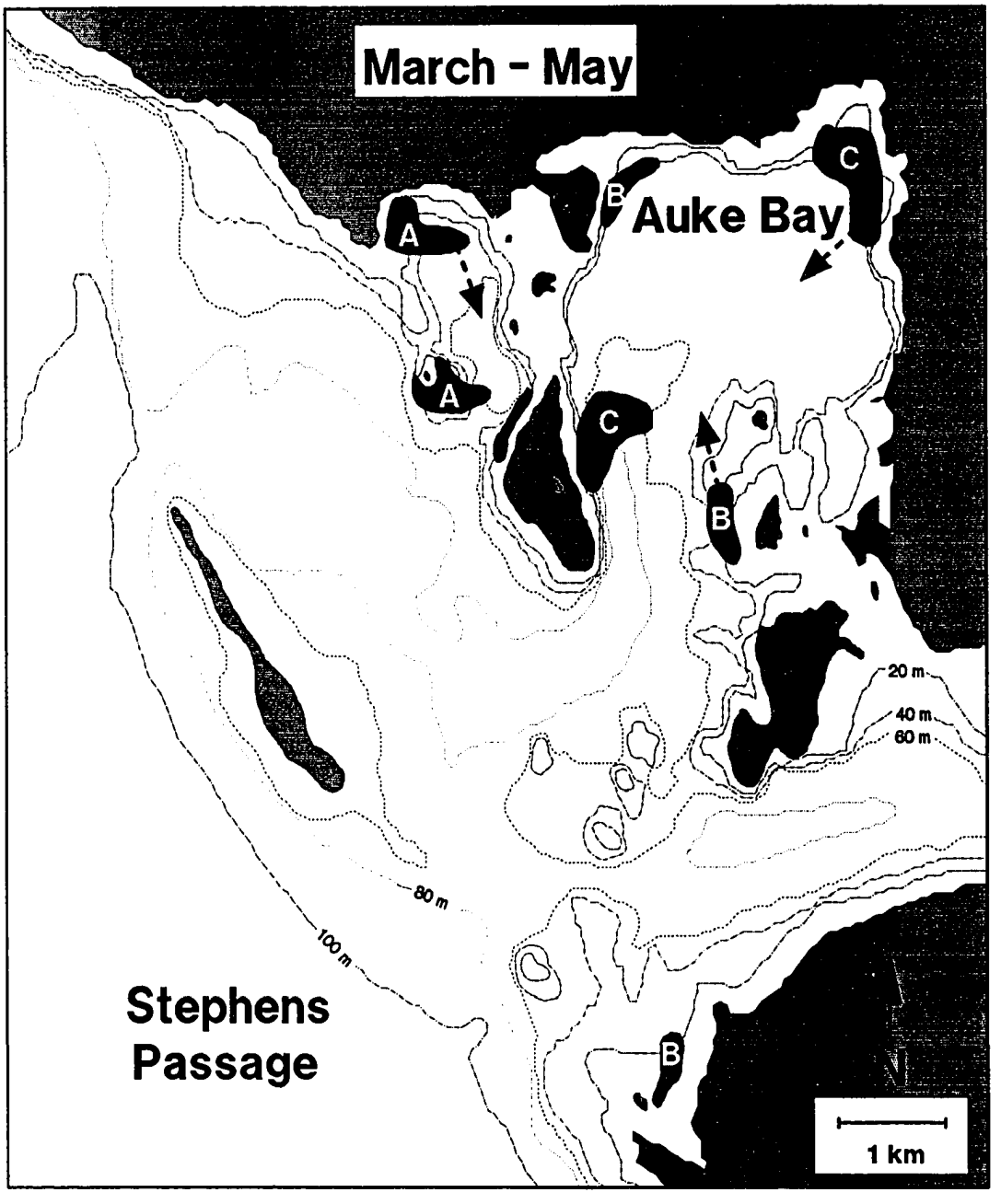


Figure 6. Areas of distribution of primiparous female red king crabs fitted with ultrasonic transmitters from March through May 1989. Arrows indicate large-scale movement. Polygons A, B, and C denote different groups of crabs whose movements are detailed in the text.

associated with the multiparous crabs within Auke Bay since August made extensive migrations to new areas prior to molting (Figure 6, polygon C). All multiparous females, except one, migrated towards the northeast corner of the bay where they ultimately molted in shallowwater areas (Figure 7). Crab No. 465A, which was the only multiparous female not initially captured near the head of the bay, remained near the shallowwater winter grounds where molting and mating eventually occurred.

The distance between the site of initial release and site of ecdysis a year later was significantly ($P < 0.001$) less for multiparous than primiparous crabs. Primiparous crabs molted 2.3-5.6 km from their release site, whereas multiparous crabs molted only 0.1-1.9 km from their release site. Although primiparous crabs molted at a wider range of depths than multiparous females (7.3-61.6 m compared to 11.6-24.1 m), these depths did not differ significantly.

General movement patterns were similar, although differences between primiparous and multiparous crabs existed when movements were examined in detail. The maximum distance crabs moved from point of release differed significantly ($P < 0.01$) between the two groups. Primiparous crabs ranged 4.5-8.6 km from point of release. In contrast, all multiparous crabs remained within Auke Bay during the entire study, and none migrated further than 4.2 km from point of release. The annual range of primiparous crabs ($\bar{x} = 11.9$ km^2) also exceeded ($P < 0.025$) that of multiparous crabs ($\bar{x} = 3.6$ km^2).

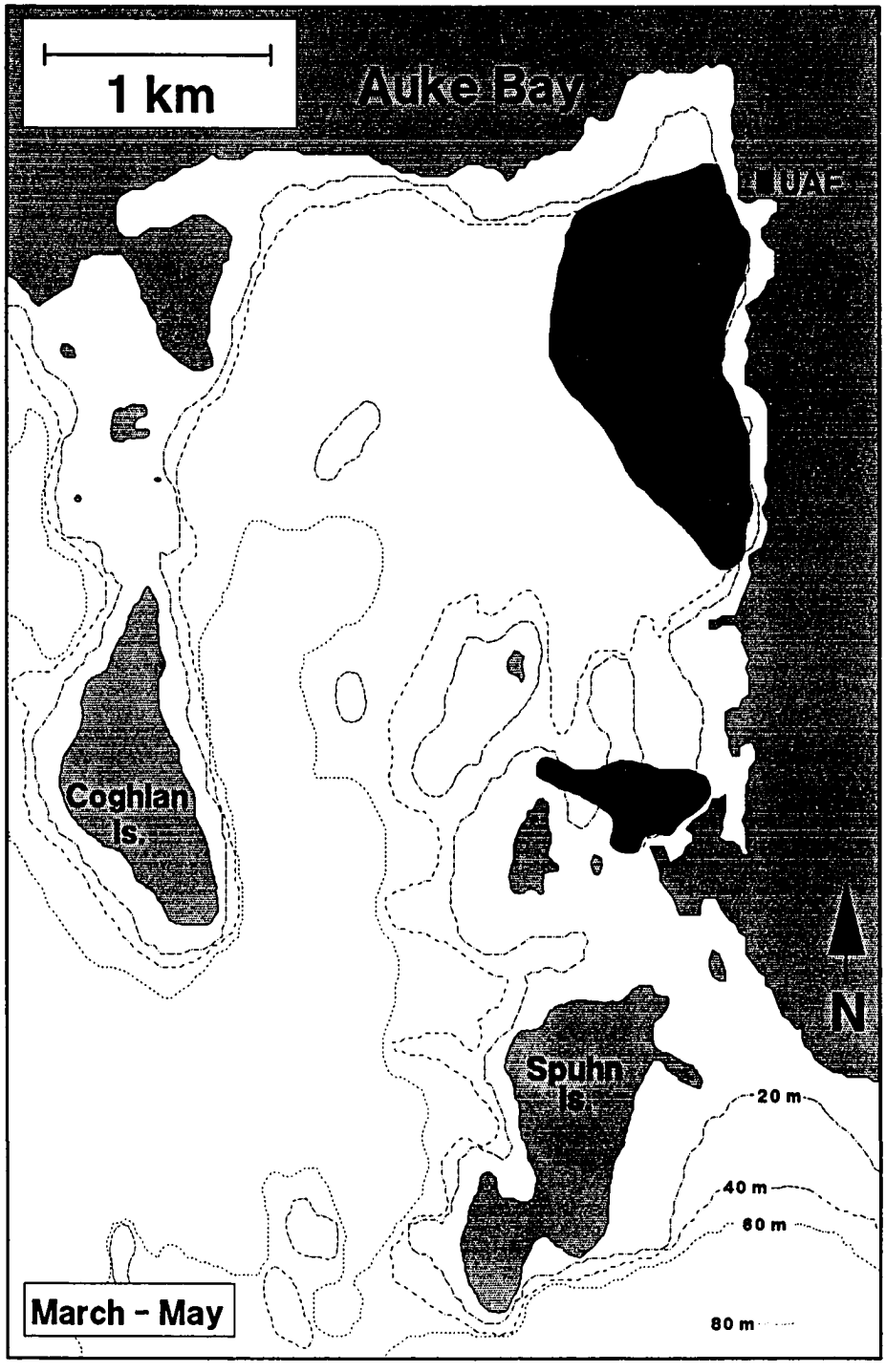


Figure 7. Areas of distribution of multiparous female red king crabs fitted with ultrasonic transmitters from March through May 1989. UAF = University of Alaska Fairbanks.

Primiparous crabs had small seasonal differences in activity rate, whereas multiparous crabs did not (Table 4). Primiparous crabs were less active in winter ($P < 0.10$, Kruskal-Wallis test) than during other seasons. Primiparous crabs were also significantly ($P < 0.05$) more active than multiparous crabs on an annual basis, but particularly during the summer/fall period ($P < 0.01$) (Figure 8).

Primiparous crabs were found at significantly ($P < 0.01$) greater depths ($\bar{x}$ = 45.6 ±1.1 m) than multiparous crabs ($\bar{x}$ = 37.4 ±2.1 m) on an annual basis (Figure 9). This was especially evident during the summer/fall period when primiparous crabs occupied mean depths of 60.5 ±3.6 m and multiparous crabs occupied mean depths of 42.2 ±1.3 m. Both groups of crabs had significant seasonal variation in depth distribution. Primiparous crabs were significantly ($P < 0.01$) deeper during the summer/fall period than subsequent periods, while multiparous females were found significantly ($P < 0.01$) shallower during the winter period (Figure 9).

Water temperature varied inversely with depth during the summer/fall period. Because of this relationship, primiparous crabs experienced small but significantly ($P < 0.001$) lower mean water temperatures than multiparous crabs (6.1 ±0.05°C and 6.5 ±0.03°C, respectively) during this period (Figure 10). Primiparous and multiparous crabs were exposed to mean annual water temperatures of 5.4 ±0.05°C and 5.5 ±0.02°C, respectively; (ranges: 3.2 - 7.3°C and 3.4 - 7.7°C, respectively).

Table 4. Mean activity rate ±1 SE, calculated as distance moved in meters divided by time in days between successive observations, of tagged female red king crabs.

Season	Primiparous	Multiparous
Summer/Fall	86.61 ±2.73	60.37 ±7.26
Winter	55.84 ±9.24	66.35 ±2.41
Spring	89.90 ±19.8	68.50 ±11.6
Annual	80.65 ±4.77	62.46 ±6.09

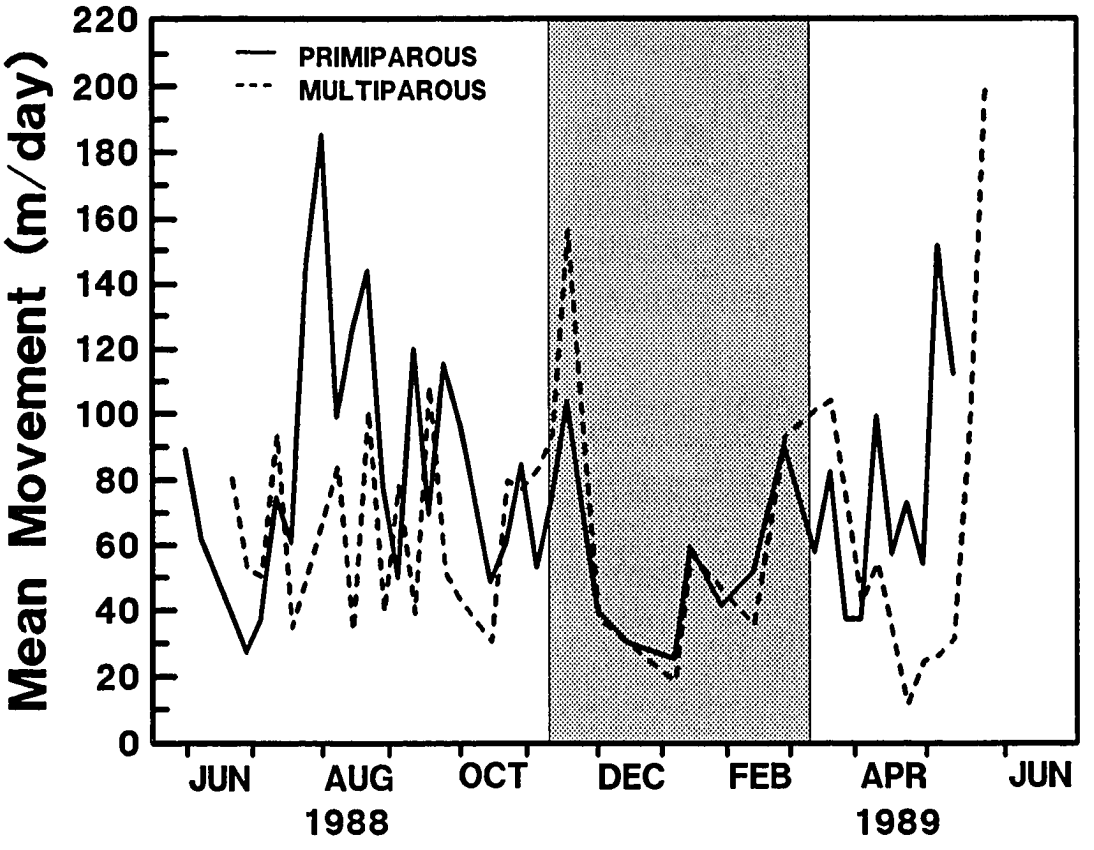


Figure 8. Activity rate (mean movement per day) for primiparous and multiparous female red king crabs fitted with ultrasonic transmitters between June 1988 - 1989. The shaded area represents the period between fall and spring thermohaline mixing.

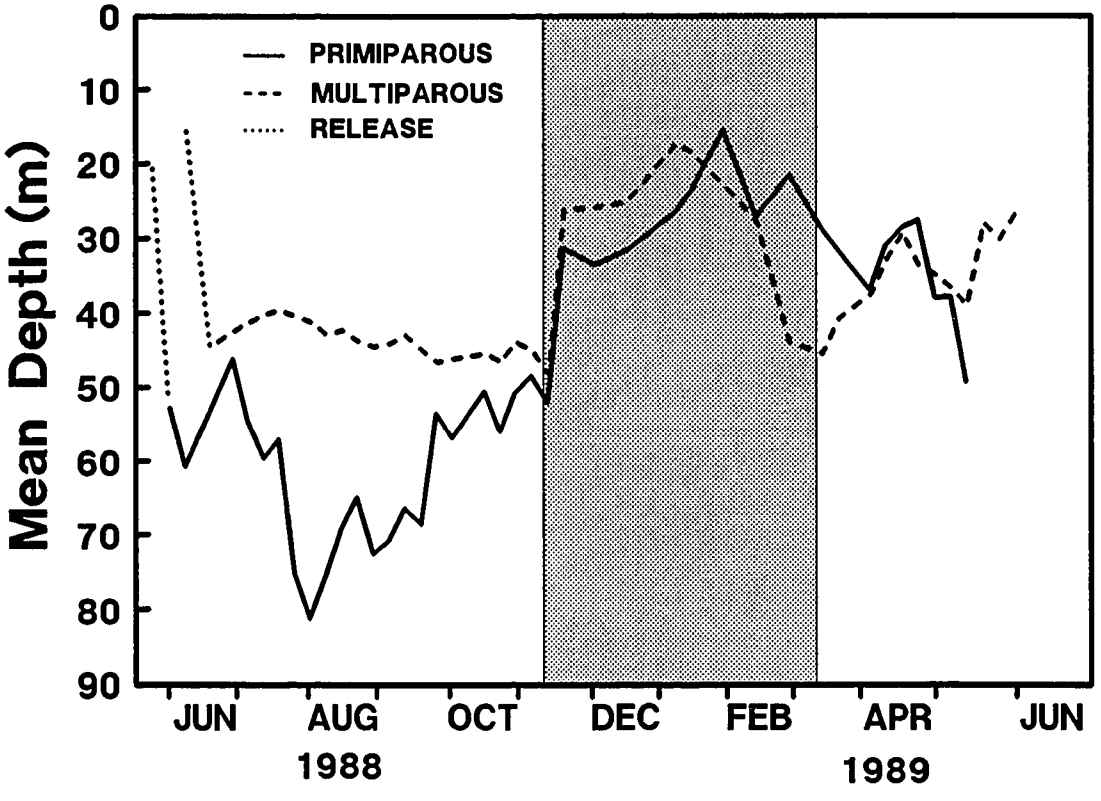


Figure 9. Mean depth of primiparous and multiparous female red king crabs fitted with ultrasonic transmitters between June 1988 - 1989. The shaded area represents the period between fall and spring thermohaline mixing.

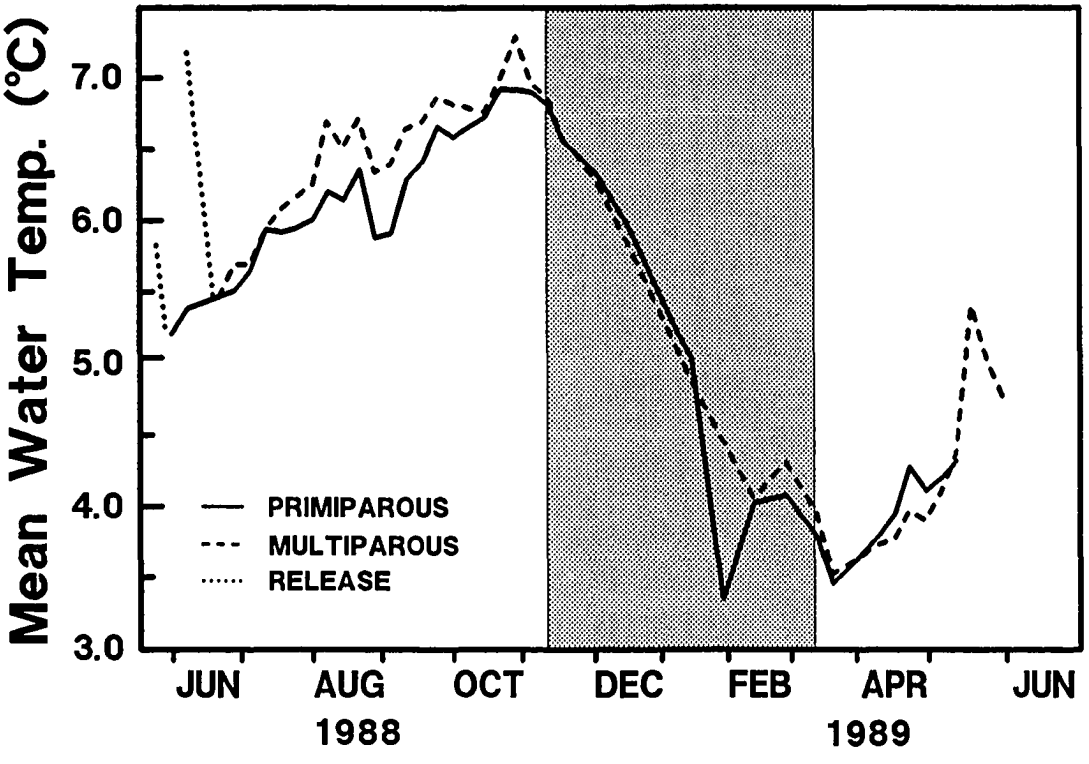


Figure 10. Mean water temperature of areas inhabited by primiparous and multiparous female red king crabs fitted with ultrasonic transmitters between June 1988 - 1989. The shaded area represents the period between fall and spring thermohaline mixing.

Primiparous crabs occupied areas with a significantly ($P < 0.05$) greater mean annual salinity than those areas occupied by multiparous crabs (31.3 ±0.02‰ and 31.2 ±0.05‰, respectively); ranges: 29.2 - 32.5‰ and 29.3 - 32.1‰, respectively (Figure 11). This was especially true during the summer/fall period ($P < 0.001$) when primiparous crabs occupied deeper, more saline areas. Both groups of crabs occupied areas of significantly ($P < 0.001$) reduced salinity ($\bar{x}$ = 30.7 ±0.08‰ and $\bar{x}$ = 30.6 ±0.10‰, respectively) during the winter period, although the physiological significance of these seasonal differences in salinity is questionable.

Mean depth of tagged crabs was directly related to photoperiod during the study period (Figure 12). In general, crabs gradually moved to shallower depths with decreasing photoperiod, and then began to migrate back to deeper areas as photoperiod began to increase after the winter solstice. Mean depth was significantly correlated with photoperiod between mid-November and mid-May ($r = 0.60$; $n = 17$; $P < 0.05$). Inclusion of data points from the previous June and early July (the period near the summer solstice) resulted in an even stronger positive correlation ($r = 0.76$; $n = 21$; $P < 0.01$) between mean depth and photoperiod. Depth distribution for crabs after 21 May was not included in the analysis due to small sample size ($N \leq 6$). Depth distribution was also significantly correlated with photoperiod during the summer/fall period ($r = 0.88$; $n = 15$; $P < 0.01$).

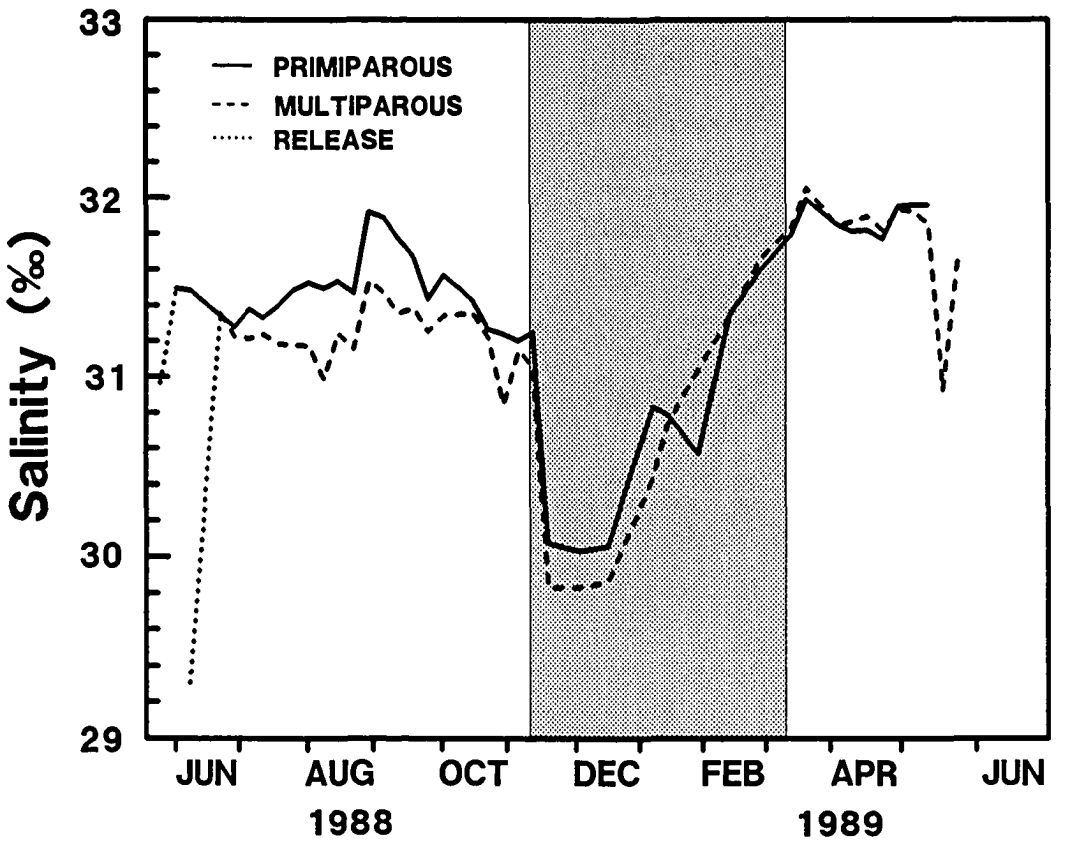


Figure 11. Mean salinity of areas inhabited by primiparous and multiparous female red king crabs fitted with ultrasonic transmitters between June 1988 - 1989. The shaded area represents the period between fall and spring thermohaline mixing.

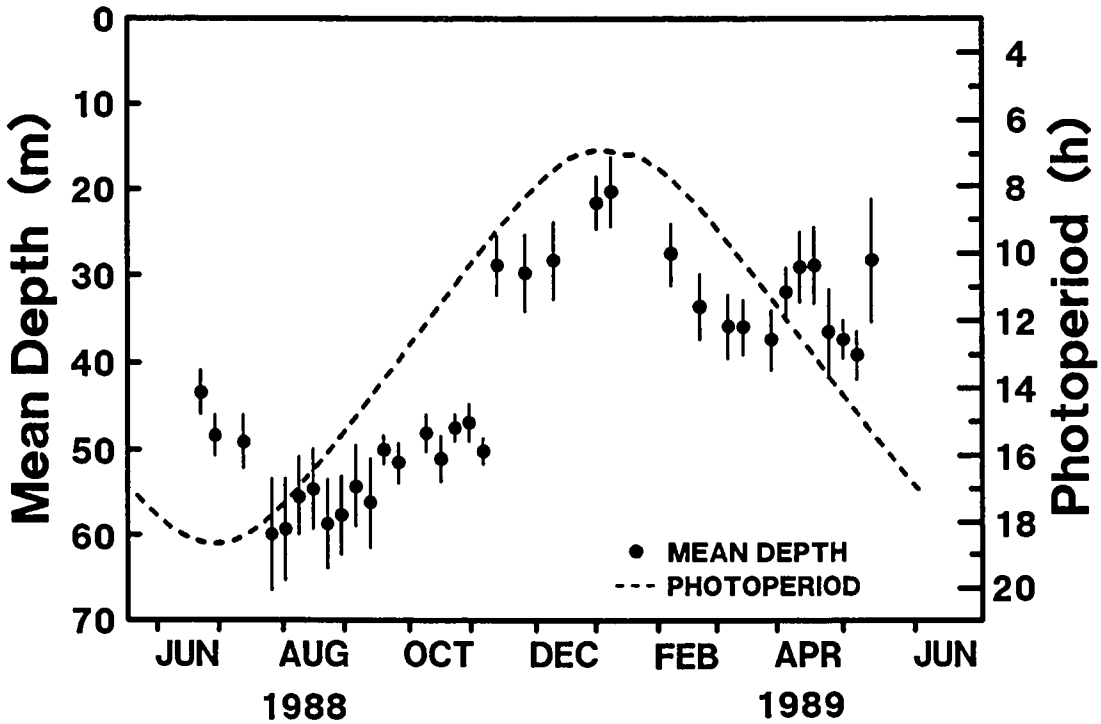


Figure 12. Mean depth (±1 standard error of the mean, SE) of female red king crabs fitted with ultrasonic transmitters relative to photoperiod between June 1988 and May 1989.

Discussion

Mark and recapture studies associated with the commercial fishery have provided researchers with the majority of data on king crab movements to date. Interpretations of these data may be misleading (Herrnkind,1980). Most tagged animals likely will be recaptured near the time and place of release, and the proportion of recaptures will depend on local fishing effort regardless of the animal's initial dispersion. A directional trend that does not actually exist might be interpreted from such data (Herrnkind, 1980).

Ultrasonic biotelemetry overcomes many of the biases associated with mark and recapture methods, in addition to providing researchers with direct and continuous data on animal movements and spatio-temporal patterns. Ultrasonic biotelemetry has received limited application in monitoring the movements and behavior of large, marine decapod crustaceans (Lund and Lockwood, 1970; Chapman *et al.*, 1975; Hill, 1978; Phillips *et al.*, 1984; Jernakoff, 1987; Wolcott and Hines, 1989, 1990; O'Clair *et al.*, 1990; Smith and Jamieson, 1991). Rusanowski *et al.* (1987) also used ultrasonic biotelemetry to monitor the movements of male red king crabs near Nome, Alaska. All of these studies have been of short duration and have focused on fine-scale or daily movements (i.e., no single animal has been tracked for more than 3 weeks). I am aware of no published studies in which this method was used to document long-term movements of any crustacean.

Tagging studies conducted in the eastern Bering Sea and near Kodiak Island indicate that males are capable of moving great distances in short periods of time (i.e., 112 km in 113 days) while undertaking extensive annual migrations (Wallace *et al.*, 1949; Hayes and Montgomery, 1963; Simpson and Shippen, 1968; Rusanowski *et al.*, 1987). Marukawa (1933) tagged both male and female red king crabs along the coast of Kamchatka and in the sea of Nemuro; red king crabs had extensive annual migrations, with the maximum rate of migration for males (13.1 km/day) exceeding that of females (10.4 km/day).

Despite the paucity of studies concerning the movements of female red king crabs, several authors compared summer distributions of adult males and females to areas of spring larval hatching (presumably near molting and mating areas), and inferred that females may not move as extensively as males (Rodin, 1970; Haynes, 1974; Stinson, 1975). Female red king crabs in the present study did not move great distances from molting and mating areas during at least one reproductive period (one year) in Auke Bay. Individuals from both groups, however, were capable of movements greater than 2 km between tracking periods (1 week).

Wallace *et al.* (1949) suggested that the magnitude of migration is governed largely by local conditions; that is, in areas with a large variation in depth, migrations may be limited, whereas in areas of uniform bathymetry, extensive migrations may be undertaken. The relatively limited distance moved from the point of release by females in Auke Bay may indicate that suitable habitat and

environmental conditions are available to these crabs within a relatively small geographical area, and that only small-scale annual migrations are undertaken by female crabs in such areas.

Except for a brief period following molting and mating, red king crabs are generally not uniformly distributed, but are believed to form distinct aggregations (Wallace *et al.*, 1949; Bright, 1967). Crabs in this study distributed themselves nonrandomly. This was especially well illustrated in the multiparous individuals. Shortly after release, the multiparous crabs spread out somewhat uniformly, then became concentrated in the eastern side of the bay. Although individual crabs often moved independently for small distances within discrete areas, large-scale movements to different areas or depths were generally undertaken as a group. The apparent preference of the multiparous crabs for the eastern side of Auke Bay remains to be explained. Bright (1967) described a similar habitat preference by red king crabs in Cook Inlet. Rodin (1970) and Stinson (1975) reported concentrations of females in the eastern Bering Sea and correlated them with increased benthic production.

Individual crabs displayed an obvious preference for certain areas or habitats to which they returned periodically. This behavior was particularly noticeable for crabs nos. 2237, 2246, 285, and 294 (see Appendices 35, 36, 40, and 41, respectively). Periodic return movements to these areas were generally highly directional and transitory. One of the most preferred areas by crabs was located

near the northeast part of Auke Bay. Crabs often were concentrated in the vicinity of the public docks near the harbor. Because this area serves as a cleaning station for local fishermen, the benthic habitat is probably often littered with fish waste. Although the orientational mechanisms involved in these movements are uncertain, crabs may have been attracted to this location by the periodic disposal of offal. This behavior would suggest that the crabs may be capable of navigating at least several kilometers by means of chemosensory cues. Crabs may also learn the guidepost features of the home-range environment, especially in smaller semi-enclosed embayments. More information is needed to determine effects of man's activities on movements of king crabs. The above observations, however, suggest that anthropogenic activities might alter or modify the movements of crabs.

Water temperature significantly affects the time required for egg incubation in the laboratory (Nakanishi, 1985; Shirley *et al.*, 1990). Regional and interannual differences in bottom water temperatures experienced by ovigerous females may, therefore, affect the time of hatching each year. Several authors have emphasized the importance of larval hatching occurring during the spring phytoplankton bloom in maximizing larval survival (Kurata, 1959; Paul and Paul, 1980; Shirley and Shirley, 1989). One possible mechanism by which female red king crabs may regulate the timing of larval hatching would be to actively migrate to areas of optimal temperature for egg incubation. Female red king crabs in this study

exposed themselves by their movements to a range of temperatures (Figure 10). They did not appear to adjust their behavior to optimize exposure to a stable thermal environment. Migratory movements may be constrained to areas of bottom within a tolerable range of temperatures, while other factors such as the availability of food ultimately controls seasonal distribution.

Food availability is likely not the sole controlling factor of these movements, however. If annual benthic production is highest in shallow water and decreases with depth in Auke Bay as it does in other estuarine communities (Warwick *et al.*, 1978), king crabs would probably exploit this increased availability of food in shallow water year-round. Since red king crabs do not occupy shallow water year-round, some other factor(s) must limit their seasonal use of these habitats.

Differences in mean annual water temperatures to which primiparous and multiparous females were exposed during this study, (5.4°C and 5.5°C, respectively), probably were not great enough to cause differential rates of embryonic development. In laboratory experiments, Nakanishi (1985) determined the optimal temperature range for developing eggs to be 3-8°C. The temperature range to which ovigerous crabs were exposed during this study (3.2 - 7.4°C) were within that range. Water temperature is more stable below the thermocline in Auke Bay (Bruce *et al.*, 1977; personal observations). If the crabs had, however, migrated to shallowwater areas, especially during the summer/fall period, they would have been subjected to temperatures far outside of this range.

Jewett and Onuf (1988) suggested that salinity rather than water temperature may regulate seasonal crab movements in areas where salinities fluctuate greatly. No information has been published on salinity tolerances and optima for adult red king crabs or the eggs in the clutches of ovigerous crabs. In their review Jewett & Onuf (1988) proposed an optimal range of 26‰ to 34‰ for adults, although they lacked supporting data. The ovigerous crabs in our study were exposed to a relatively narrow range of salinities (28.3 to 32.5‰) within the range suggested by Jewett & Onuf (1988) as optimal for adult red king crabs. The salinity at depths greater than about 12 meters in Auke Bay is nearly constant between 30‰ and 31‰ annually (Bruce *et al.*, 1977). Salinities at depths less than 12 meters are generally outside the range suggested by Jewett and Onuf (1988) between June and August only, that period when all crabs in this study were found at depths greater than 40 m. Although salinities at depths occupied by crabs in this study were quite stable (Figure 11), salinity may regulate movements by preventing crabs from using shallow habitats in summer when salinities there are markedly reduced.

Somerton (1985) noted that red king crabs near Kodiak Island were never found shallower than the seasonal thermocline, but often directly below it. Except for a brief period when thermohaline mixing began in October, this relationship was also observed for female red king crabs in this study (Figure 13). Female red king crabs in Auke bay also always occupied depths below the seasonal halocline (Figure 13). The strength of the thermocline changes considerably from month

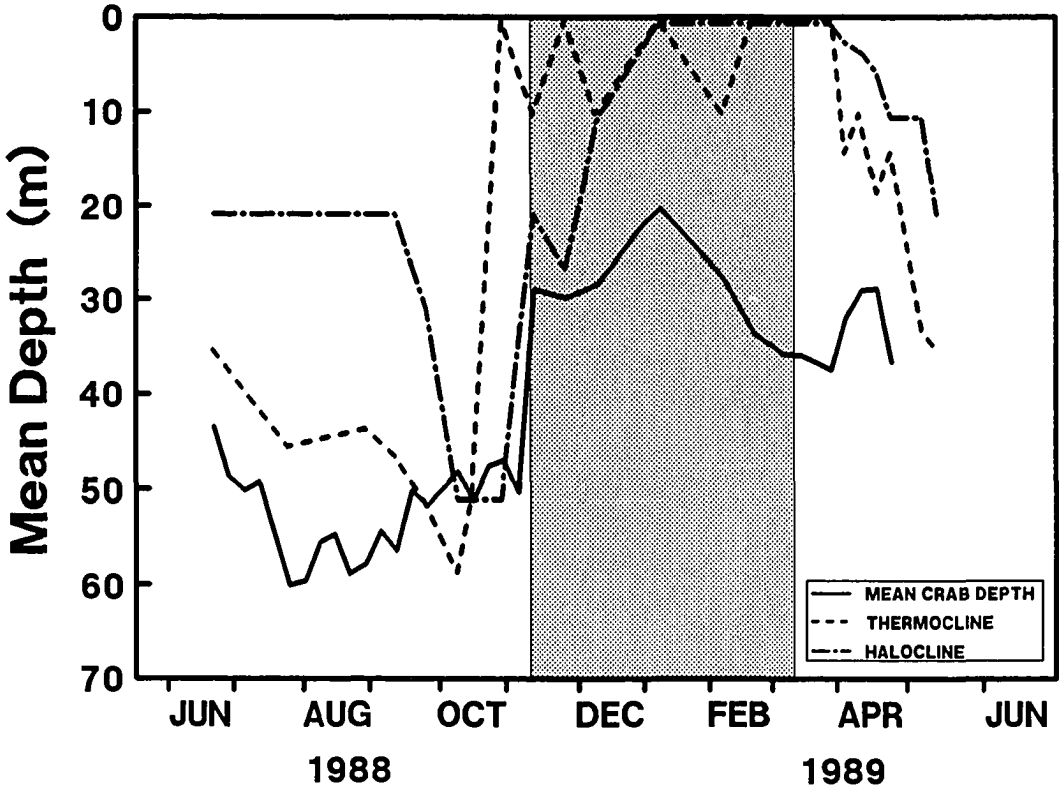


Figure 13. Mean depth of female red king crabs fitted with ultrasonic transmitters relative to the lower limits of the thermocline and halocline zones between June 1988 and June 1989. The shaded area represents the period between fall and spring thermohaline mixing.

to month in Auke Bay. For example, a 9°C differential between the surface and lower limit of the thermocline was observed during the summer and fall, while the differential for the shallow (< 10 m) thermocline infrequently present during winter months seldom exceeded 1°C. A similar seasonal pattern for the strength of the halocline also exists. The abrupt, synchronous movement of crabs in November, and to a lesser degree in March, was coincident with thermohaline mixing of the water column in Auke Bay. A similar, albeit opposite, movement has been described for *Panulirus interruptus* during autumn off the southwest coast of North America (Mitchell *et al.*, 1969). King crabs in this study moved into the shallow water areas as the thermocline/halocline decayed. The thermocline or halocline may act as a barrier to restrict the movement of king crabs from the summer/fall feeding grounds to the food-rich, shallowwater, winter feeding grounds. The crabs departed these shallowwater areas as the thermocline and halocine began to develop again in March. These coincident events require further study to postulate a functional relationship, however, as thermocline/halocline formations are correlated with other environmental variables, such as photoperiod.

Despite the known relationship between migration and temperature in a few decapod species (Bainbridge, 1961; Allen, 1966; Dorgelo, 1976), the direct effects of temperature changes on movement patterns and seasonal activity rhythms in marine crustaceans remains unknown (Kanciruk and Herrnkind, 1978). The

abrupt, synchronous movement of crabs in this study, although coincident with thermohaline mixing, was apparently not associated with rapid temperature changes in areas where crabs were concentrated.

The influence of photoperiod on seasonal migrations has been well documented for many animals, especially birds and insects. Baggerman (1960) proposed that internal neuro-endocrine processes and rhythmicity in fish are stimulated by long-term cyclic changes in photoperiod or temperature, and migration is initiated by other factors which act on this modified physiological state. Depth distribution of female red king crabs in this study were highly correlated with photoperiod during the summer/fall period when mean crab depth was greater than 45 m. Adult anomurans possess superposition eyes which are highly modified in some species for maximum sensitivity (Herring and Roe, 1988). Although the crabs in this study were at depths receiving far less than 1% incident light (generally 10-20 m depth in Auke Bay) (Wing, 1976), they were probably able to detect these low light levels, and hence photoperiod. Red king crab zoeae respond to light intensities as low as 1.3 X 10^{11} q cm^{-2} s^{-1} (Shirley and Shirley, 1988a). The mean light intensity at 15 m depth at Auke Bay is more than 1 x 10^5 times greater than this value on bright days (Tom Shirley, personnel observations).

Two fundamental questions concerning the migration of animals are; 1) what are the clues used by migrants when enroute and how do they recognize a particular area or habitat upon arrival, and 2) what are the cues that temporally

integrate migratory movements and behavior with seasonal changes in the environment (Harden-Jones, 1980). In this context, the decay of the thermocline in fall may serve as a clue for red king crab indicating that conditions in shallow water are favorable. Autumnal decreases in photoperiod might serve as a cue, which coordinates behavior with these changes in conditions and induces the onset of migratory behavior. If thermohaline mixing is a predictable event interannually and red king crabs are capable of detecting fine-scale changes in photoperiod, then king crabs might only need to periodically "sample" the surrounding water column to determine when conditions are favorable in shallow water.

Although mean crab depth is also significantly correlated with photoperiod between mid November and early July, the relationship deteriorates somewhat during April and May when females move into shallow water to molt and mate. Because the timing of movement back into shallow water is not completely synchronous and is size-dependent, it is probable that other factor(s) acting in concert with photoperiod are responsible for these movements. Some marine invertebrates respond directly to phytoplankton blooms and use them as spawning cues (Starr *et al.*, 1990). Critical density levels of phytoplankton might indicate when existing conditions are favorable for larval hatching and induce movements into shallow water.

Results from this study substantiate and extend the work of Powell and Nickerson (1965a) which indicated that female red king crabs tend to aggregate

in discrete areas during certain times of the year, presumably for feeding or reproduction. Observations by divers confirmed that aggregations in shallow water were composed of both primiparous and multiparous females between November and March. Distributions of tagged primiparous and multiparous crabs also overlapped during the summer/fall period. I could not locate areas where both size classes co-occurred during April and May, and therefore conclude that only the timing of the spawning migration and onset of the feeding migration differs for these two groups.

Such a spatio-temporal shift could have important ecological and evolutionary implications for this species, where synchrony of larval hatching and spring phytoplankton events are critical for larval survival. The duration, magnitude, and to a lesser extent, timing of spring phytoplankton blooms vary interannually in systems such as Auke Bay (Ziemann *et al.*, 1990). If red king crab larvae hatched over several months, at least a percentage of all zoeae hatched would encounter conditions promoting maximum survival.

Primiparous females might benefit from this reproductive strategy (one in which mating is not synchronous). Natural selection might favor earlier mating in primiparous crabs if males were a limited resource and competition for mates occurs among females. Primiparous crabs would increase their individual fitness by mating earlier than multiparous crabs.

CHAPTER III.

PODDING BEHAVIOR OF OVIGEROUS FEMALE RED KING CRABS IN AUKE BAY, ALASKA

Introduction

Red king crab (*Paralithodes camtschaticus*) larvae metamorphose into the adult form following a 45-60 day pelagic period and adopt a benthic existence (Marukawa, 1933). Juveniles are solitary during their first year of benthic life and lead a cryptic existence occupying protected refuges in the shallow subtidal zone (Sundberg and Clausen, 1977). In contrast, subsequent age classes (1-3 years old) often form dense aggregations in the eulittoral and shallow sublittoral zones (Durham, 1960; Bright *et al.*, 1960; Powell and Nickerson, 1965b; Dew, 1990). These dense aggregations, or pods, may be composed of several hundred to thousands of individuals.

The carapace lengths of podding red king crab in the Kodiak Island area range between 24 and 69 mm (Powell and Nickerson, 1965b). Juvenile red king crabs initially form pods during their second year, therefore, and continue to display this highly structured behavior as four year olds. Although Bright (1967) suggested that pods may be comprised of mixed age classes, Powell and Nickerson (1965b) report that age classes do not intermingle and probably occupy distinct biological niches.

The distribution of four and five-year-old red king crabs is poorly known. Aggregations of these age classes have not been observed in shallow water and individuals are infrequently caught at depth by conventional sampling methods. Powell and Nickerson (1965b) proposed that these age classes intermingle and probably inhabit intermediate depths (18-30m). Vinogradov (1969), however, reported that these age classes have a similar distribution to adults along the western Kamchatka shelf.

Red king crab attain sexual maturity at five to six years of age over most of their geographic range (Bright *et al.*, 1960; Weber, 1965; McMurray *et al.*, 1984), after which time they undertake seasonal onshore-offshore migrations thought to be directly associated with reproduction and feeding, respectively (Wallace *et al.*, 1949; Bright, 1967). The sexes are believed to be segregated during these migrations and to form discrete groups, separated by age and sex, during much of the year (Wallace *et al.*, 1949; Bright, 1967), although supporting data are weak or non-existent.

Adult red king crabs are thought to display gregarious behavior similar to that of early age classes, but podding behavior in adult crabs has been reported only twice (Powell and Nickerson, 1965a; Jewett and Powell, 1981). These accounts suggest that males and females independently form aggregations preceding mating in shallowwater areas. Early commercial and scientific observations suggested that

adult red king crabs are generally not uniformly distributed, but rather exhibit a somewhat contagious distribution (Wallace *et al.*, 1949).

The red king crab fishery was one of the most valuable on record until drastic declines in population levels resulted in a complete closure of the fishery in 1983 (Blau, 1986; Otto, 1986). Although the high resource value provided much incentive, the aggregated distribution of red king crabs may have contributed to the high exploitation rates that helped make this fishery so lucrative.

The deductions concerning the spatial pattern of red king crab are based on remote sampling techniques (i.e., trawl and pot surveys), which might introduce untestable bias and lack fine-scale details of spatial patterns. Hsu (1987) reviewed the results of the groundfish trawl surveys conducted by the National Marine Fisheries Service (NMFS) between 1972 and 1985 in the southeastern Bering Sea and concluded that females have a highly aggregated distribution at a very large spatial scale. These surveys were conducted over a six-week period in June and July each year, over vast areas, with single samples from 400 square mile quadrats, and consequently provide little insight into seasonal distribution patterns.

The purpose of this study was to determine the seasonal distribution of one population of female red king crabs and to provide direct documentation of the sex and size-class composition of adult red king crab aggregations. This study also characterizes the benthic habitat utilized by mature female red king crabs on a temporal scale.

Materials and Methods

This study was conducted in the vicinity of Auke Bay, located 19 km northwest of Juneau, Alaska (Figure 14). Auke Bay is a small estuary which supports a local sport fishery for red king crabs. Red king crabs are also common in the waters near Auke Bay. The physical and chemical oceanography of the study area have been described in detail by Bruce *et al.* (1977).

Ovigerous female red king crabs were collected with baited pots and by divers at three locations within the bay. Ultrasonic transmitters with a two-year life expectancy were attached to ten crabs from each of two distinct size-classes; primiparous females or those reproducing for the first time and multiparous females which had spawned at least once previously. Two additional crabs were tagged during the study when derelict tags (i.e., tags which became detached from crabs) were recovered by divers. Tag specifications and tagging methods have been described (pp. 13-16, chapter II); laboratory and field observations confirmed that tagged crabs do not show signs of stress or modified behavior.

Primiparous and multiparous crabs were released on 17 May and 3 June 1988, respectively, in areas close to their initial capture. The positions of the crabs were usually determined weekly, as weather permitted, using an ultrasonic receiver (Sonotronics model USR-4D) and directional hydrophone (Sonotronics model DH-2). A small float was deployed after the boat was positioned over a crab.

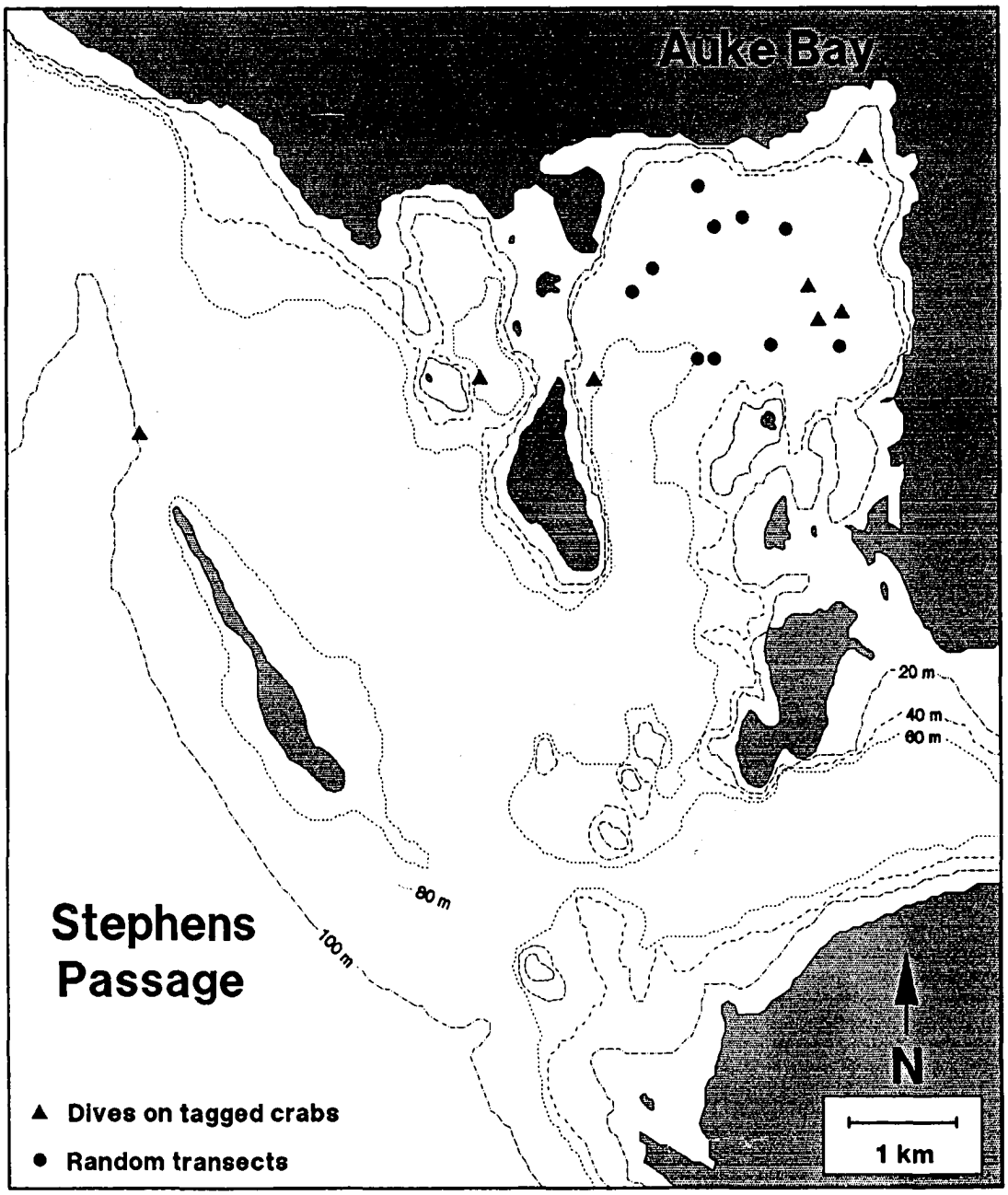


Figure 14. Study area at Auke Bay, Alaska; circles indicate sites where dives were made on random transects, and triangles denote sites where dives were made on tagged crabs. Dives were made in the research submersible Delta. Depth contours are in meters.

The boat was maintained at this float while its position was fixed by measuring angles between three shoreward markers with a beam converging sextant (O'Clair *et al.*, 1990). Depth was measured with a Hummingbird Model 4080D depth finder, and is reported as meters relative to mean lower low water (MLLW).

When two or more crabs occupied areas very close to each other (within 10 m), determining separate positions was often impossible. During the twelve weeks this occurred, a general position was recorded for the group of crabs, and all crabs except one were randomly assigned positions (a bearing and maximum distance of 10 m) from the general fix.

Several tests of spatial randomness using mean nearest neighbor distances have been developed and have received widespread application in ecological studies (see Sinclair, 1985). Weekly positions of crabs were plotted with a microcomputer design and drafting program (Autodesk, 1988), and the distance between each crab and its nearest neighbor was measured. A one-way analysis of variance (ANOVA) with 1000 random permutations (Edgington, 1987) was used to determine if the mean nearest neighbor distance changed seasonally. Fisher's modified least significant difference method (modified LSD) was used to determine significance of post hoc comparisons (Edgington, 1987). This analysis included all tagged crabs within inner Auke Bay except those which were 500 m or more from their nearest neighbor. These crabs were considered outliers on the basis that, although they may have been associated with untagged crabs, they were

not part of the aggregation under study. Zero to four outliers were excluded weekly based on these criteria (15.4% of the total number of observations), and the number of weekly outliers had no apparent seasonal trend.

SCUBA was used to make observations of tagged crabs when they were within diving depth (< 35 m) and to recover molting tagged crabs during spring. Divers used a submersible receiver/hydrophone (Sonotronics model USR-88) to locate tagged crabs underwater. Divers recorded observations including number of crabs sighted, density and structure of aggregations, sex and size (age-class) composition, depth, activity (i.e., feeding, molting, mating), and habitat characteristics including substrate composition, bottom topography and biota.

In spring 1989, two primiparous and four multiparous females were retagged. Twenty additional crabs were tagged between May 26 and June 7: the mates of the four retagged multiparous females, two clasping pairs, six single males, and six single females. All crabs were released close to the area of capture. Although these crabs were tagged primarily for the submersible study described below, the general locations of several of the crabs were periodically recorded through spring 1990.

Between 11 and 15 June 1989 twenty-four dives were made in the two-man research submersible Delta. The submersible had a length of 4.6 m, 19 viewports, and an operating depth of about 350 m. Delta was generally operated in direct contact with the sea bottom, but did not seem to affect the behavior of any

observed king crabs. Ten quadrats were randomly selected from a 10 X 10 grid superimposed over Auke Bay (Figure 14), and the submersible was directed along a transect of predetermined bearing also selected randomly. These transects were estimated to be 150 m in length (300 seconds @ average speed of 0.5 m/s). Observations were visually recorded from both sides of the submersible and videotaped by the observer.

Seven dives were also made in the vicinity of crabs tagged in spring 1989 (Figure 14). A submersible hydrophone was affixed to the compass staff on the bow and the pilot directed the submersible towards a tagged crab. Observations were made while searching for the tagged crabs, after which time crabs would be enumerated along a random transect as above. Four additional dives were made to survey and characterize deep-water habitat where crabs from the 1988-89 study were concentrated.

Results

The movements and distribution of seven primiparous and five multiparous females tagged and released in spring 1988 were monitored through one complete reproductive cycle (11-12 months). The remaining ten crabs tagged in spring 1988 were tracked between 18 and 300 days after release (Appendix 45).

Except for a brief period following release, female red king crabs in this study displayed nonrandom distribution. This pattern was especially evident in the multiparous females released near the head of Auke Bay. Although individual crabs often made treks for short distances within discrete areas, large-scale movements to different areas or depths were generally undertaken as a group. All multiparous females remained within Auke Bay and none migrated further than 4.17 km from point of release.

Primiparous females were released near outer Auke Bay and had split into two main groups by mid-summer. One group of four crabs moved out of the bay into adjacent Stephens Passage. A second group of four crabs moved into the inner bay and occupied areas adjacent to and often overlapping those occupied by multiparous crabs. The Stephens Passage group was generally distributed as two groups of two crabs. Large-scale movements within these two groups were remarkably well coordinated. Although the direction and magnitude of movements by these two groups were similar, tagged crabs seldom interacted

between groups suggesting that they may have been two distinct aggregations of crabs.

Three seasons were delimited for this study based on crab movements and physical oceanographic cycles as follows: 1) a summer/fall period from June through mid-November, when crabs inhabited deep waters ($\bar{x}$ = 52.6 m) below a well developed thermocline; 2) a winter period from mid-November through early March, when crabs inhabited shallow waters ($\bar{x}$ = 27.5 m) and when the water column was well-mixed and essentially homogeneous with respect to temperature and salinity; and, 3) a spring period from early March through late May marked first by crab movement to intermediate depths ($\bar{x}$ = 33.5 m) and then by movement into shallow water to molt and mate in April/May. This period was also characterized by the redevelopment of the thermocline and halocline during late March.

Female red king crabs in this study had distinct seasonal shifts in habitat use (Figure 15). Primiparous and multiparous females had remarkably similar patterns of seasonal habitat use. Was this shift in seasonal habitat use accompanied by a corresponding shift in the degree of crab aggregation? Female red king crabs tended to be significantly (mean nearest neighbor distance, $P < 0.01$) more aggregated during the winter than during summer/fall (Figure 16). Females were not, however, significantly ($P > 0.05$) more aggregated during the

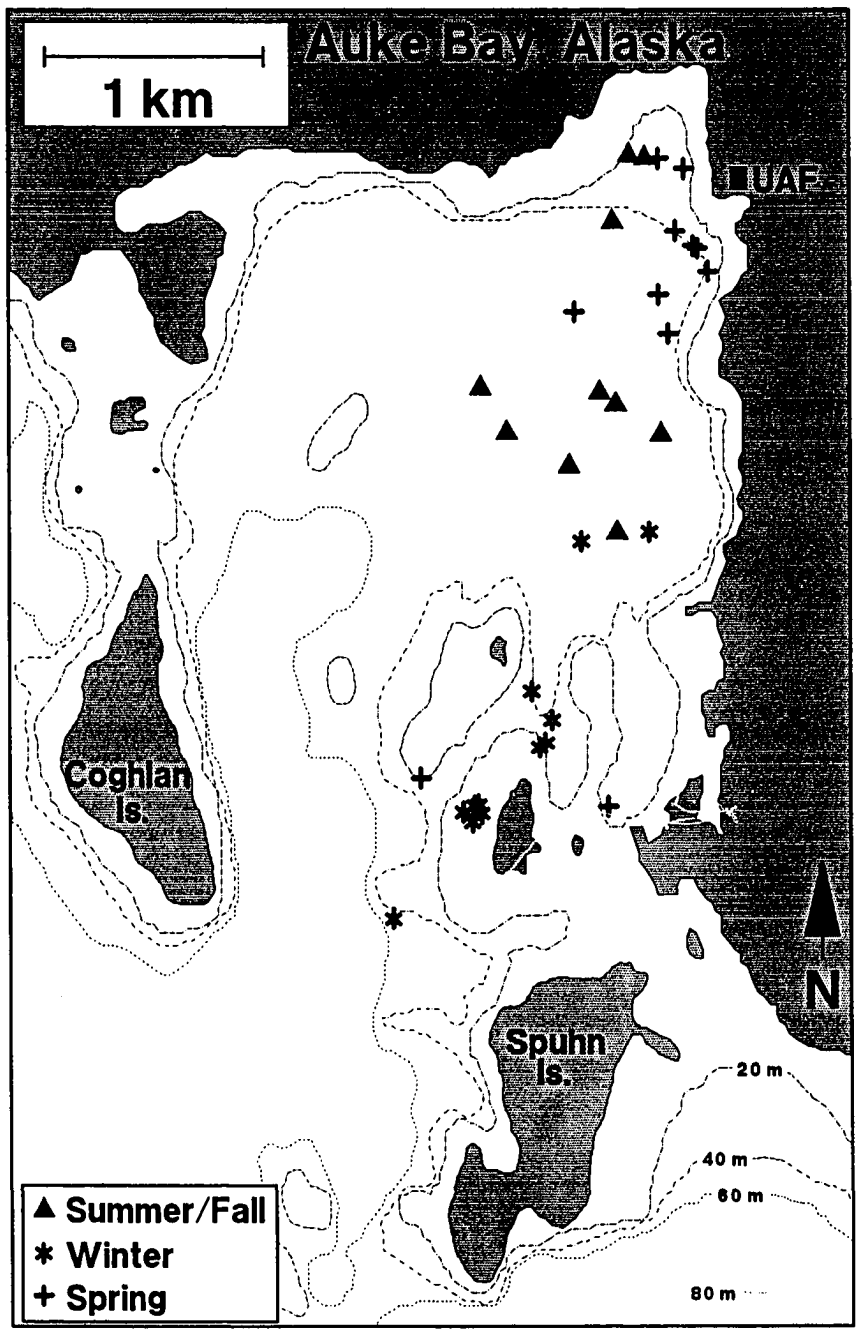


Figure 15. Map of study area showing the distribution of all tagged female red king crabs within Auke Bay during a typical week from each of three seasons. Summer/fall is represented by positions fixed between 23 and 25 August 1988. Winter and spring are represented by fixes on 12 and 13 December 1988 and 30 March 1989, respectively. Depth contours are in meters.

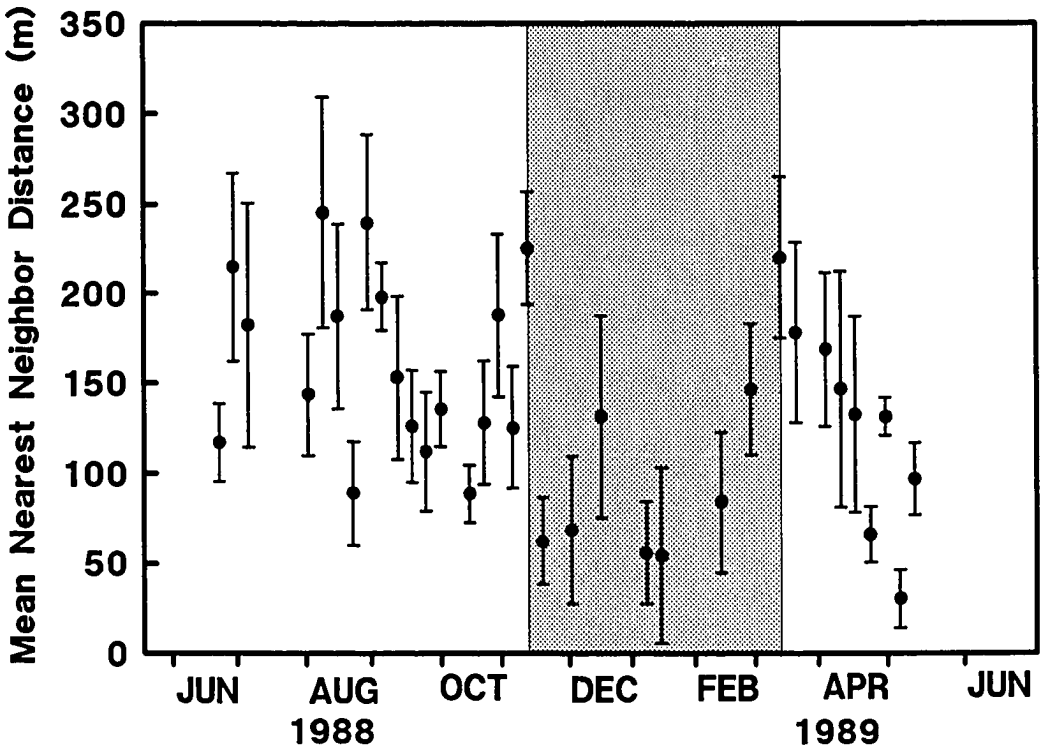


Figure 16. Mean nearest neighbor distance (±1 standard error of the mean, SE) for all crabs within inner Auke Bay (outliers were removed). The shaded area represents the period between fall and spring thermohaline mixing.

winter than in spring, nor were there any significant ($P > 0.05$) differences between summer/fall and spring dispersion patterns (Figure 16).

During winter tagged females were tightly aggregated, and individual positions could not be determined for these crabs on seven occasions. The number of tagged crabs occupying the same position ranged from two to seven, and the same individuals often remained together for extended periods (i.e., four crabs remained within the same group between 18 November 1988 and 13 January 1989). This situation also occurred four times during summer and three times during spring, but only once involved more than two crabs. These crabs, however, never shared the same position during consecutive weeks.

Diver observations during winter revealed that tagged females were often associated with dense aggregations estimated to consist of 300 or more individuals. Movement patterns for two distinct aggregations tracked for 81 and 77 days during this period are detailed in Figure 17. Aggregation 1 was considered to be a stable aggregation on the basis that between four and seven tagged crabs remained together for a period of several months. In addition, several dives made during this period indicated that tagged crabs were always part of a much larger aggregation. Although aggregation 2 consisted of only one tagged crab, I contend that this crab was part of a large aggregation between 12 January 1989 and 30 March 1989. During this period, diver observations confirmed that this crab was always found in the presence of several hundred other crabs. I further maintain

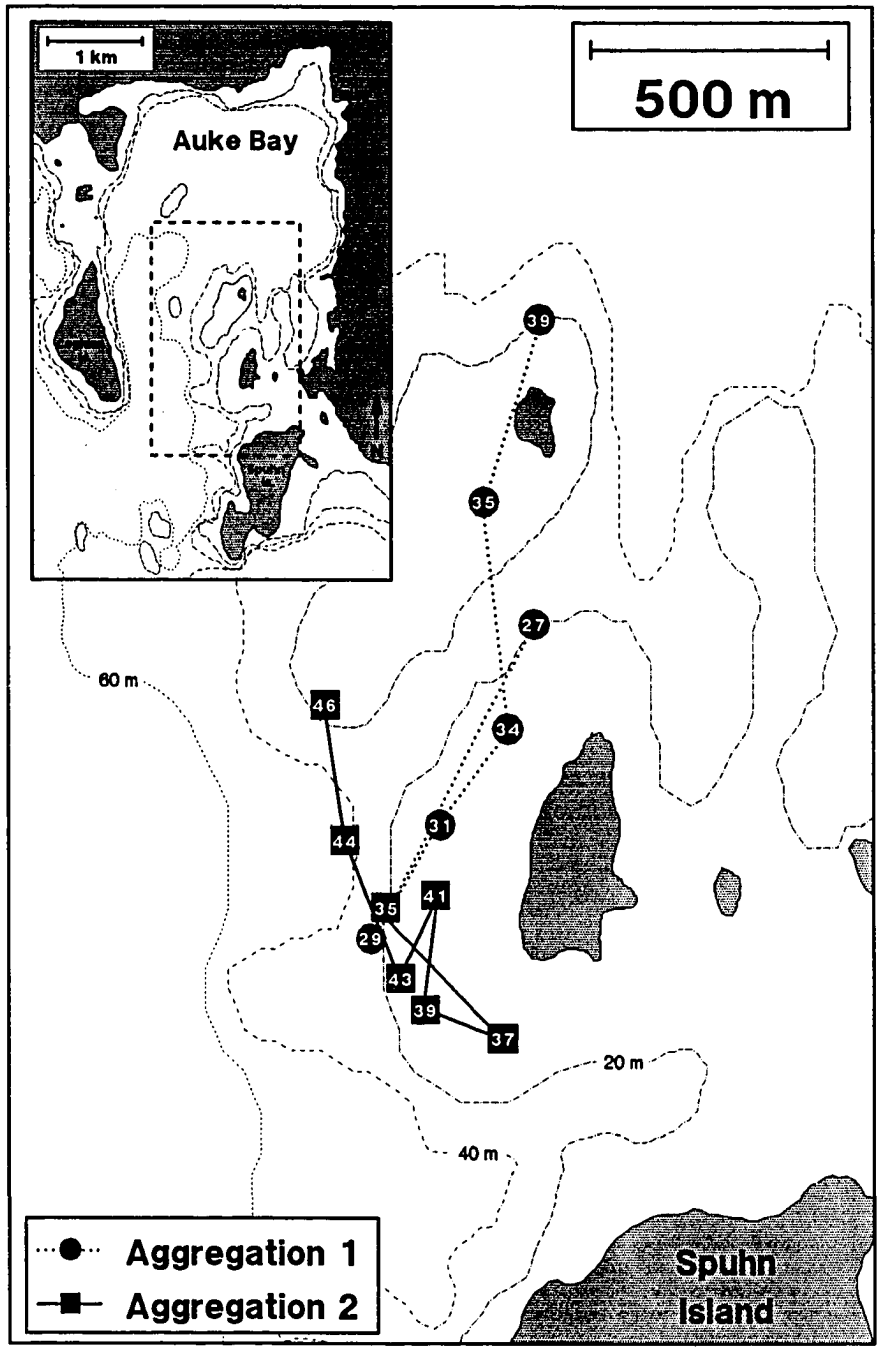


Figure 17. Movements of two aggregations of female red king crabs tracked between 18 November 1988 and 30 March 1989 in Auke Bay, Alaska. Symbols denote weekly locations; numbers denote week of study period.

that it was a stable aggregation on the basis that the tagged crab (and presumably the same association of crabs) occupied the same general area and had very limited movements during this period (Figure 17).

Although movement patterns and habitat use were remarkably similar for these two aggregations, they were temporally and spatially separated and considered distinct aggregations on that basis. In addition, no exchange of tagged crabs between the two groups was observed. Aggregation 1 was first observed on 18 November 1988 and was tracked until 7 February 1989, when crabs apparently disbanded somewhat and moved to intermediate depths. This aggregation moved a total distance of 2,169 m, had a mean movement rate of 27 m/d, and occupied shallow areas with a mean depth of 15.5 m. Aggregation 2 was first observed on 12 January 1989 and was monitored through 30 March 1989, after moving a total distance of 1,695 m. This group of crabs had a mean movement rate of 22 m/d, and a mean depth of 19.1 m. Total displacement (straight-line vector distance from first to last positions) for these aggregations were 710 m and 495 m, respectively. Tracking records for these two aggregations are presented in Table 5.

Aggregations in shallow water (mean depth < 20 m) comprised both primiparous and multiparous females, although multiparous females always predominated. On several occasions, crabs were stacked three or four deep and pods were structurally similar to pods of juveniles. These pods were often closely

Table 5. Tracking records for two aggregations of female red king crabs tracked in Auke Bay, Alaska.

Week No.	Date	Distance Moved (m)	Depth (m)	No. of Tagged Crabs
		Aggregation 1		
27	11/18/88	------	18.6	4
29	12/02/88	735	23.5	4
31	12/13/88	283	8.5	5
34	1/06/89	255	11.0	7
35	1/13/89	478	11.6	7
39	2/07/89	417	19.5	6
		Aggregation 2		
35	1/12/89	------	15.9	1
37	1/26/89	369	9.5	1
39	2/07/89	199	11.3	1
41	2/22/89	260	8.5	1
43	3/06/89	225	19.5	1
44	3/14/89	328	53.0	1
46	3/30/89	314	16.2	1

associated with a reef-type structure, and usually stacked up against it. Most crabs in the vicinity of an aggregation were closely associated with it, as evidenced by the small number of crabs found as divers swam away from an aggregation.

Although females were generally inactive with their walking legs and abdomens partially buried in silt, feeding was observed on several occasions. Crabs were observed feeding on *Pycnopodia helianthoides*, *Evasterias troschelii* and *Balanus* species. Males were observed with these shallowwater aggregations as early as mid-January, but no mating was observed before late February. Clasping pairs consisting of large, legal-size (CL > 145 mm) males and virgin females were observed near the periphery of these aggregations into early March, after which time most females had migrated to intermediate depths. A few tagged crabs remained in shallowwater areas, however, and diver observations confirmed that females continue to form aggregations through late March. Although large males were often found near these aggregations, no molting or mating was observed. Dense aggregations of crabs were not observed after 31 March, and diver observations suggest that females generally disband into loosely aggregated groups of up to sixty crabs until molting and mating occur.

Near-bottom visibility from the manned submersible Delta was often less than one meter, and likely contributed to the limited number of red king crab observations in deep water habitat. No red king crabs were observed along transects in randomly chosen quadrats of Auke Bay (Figure 14). Tanner crabs

(*Chionoecetes bairdi*), however, were observed along six of ten transects. Three red king crabs fitted with ultrasonic transmitters were located from the research submersible, and both untagged red king crabs and Tanner crabs were observed in the vicinity of those tagged crabs. Although attempts to locate and observe four other tagged crabs from the research submersible failed, untagged red king crabs were observed in the vicinity of two of those crabs.

Discussion

This study provides the first detailed documentation of "podding" behavior for adult red king crabs. Podding behavior in juvenile red king crabs was first observed in 1958 (Bright *et al.*, 1960), and has been well documented over the past thirty years. Although there are a few published accounts of podding behavior in adult red king crabs (Powell and Nickerson, 1965a), the behavior is generally considered to be unique to juveniles. Podding behavior of adults is probably less conspicuous because they undertake seasonal migrations and occupy depths accessible to SCUBA during only part of the year.

Although the small number of observations in this study precluded use of tests of spatial randomness, the ultrasonic telemetry methodology provided insight into spatial distribution patterns of adults. Distribution patterns of tagged females during the summer and fall suggest that they are not uniformly distributed, but tend to form loosely-knit feeding aggregations within fairly well-defined areas. Data gathered from the research submersible supported this hypothesis. Only thirteen red king crabs were sighted from the submersible; all of these sightings were made in the immediate vicinity of tagged crabs. No red king crabs were observed along the transects in randomly chosen quadrats of the bay, where no tagged crabs were present. Poor visibility at depth likely contributed to the small number of sightings. Tanner crabs were observed on 60% of the random

transects, however, suggesting that king crabs would also have been encountered if they were present along those transects. Rusanowski *et al.* (1987) conducted video surveys with a remotely operated vehicle (ROV) near Nome, Alaska, and sighted only four red king crabs along 2250 m of transect, implying that red king crabs were not randomly distributed there.

Whether or not adults form dense aggregations below diving depth remains unresolved, although analysis of mean nearest neighbor distances would suggest that this behavior is more typically a shallowwater phenomenon (Figure 16). Powell (1974) also suggests that adults probably do not form pods at depth due to the increased amount of time they spend foraging during adulthood. This behavior could also be related to prey distribution and abundance patterns, however.

Because diver observations confirmed that tagged crabs were often closely associated with other crabs, the telemetry methodology permitted frequent observations of crab aggregations in shallow water by remotely monitoring the movements of only a few individuals from the surface. These aggregations generally formed in areas seldom visited by divers and probably would have gone unnoticed without the aid of biotelemetry.

The advantages of a highly aggregated distribution for adult red king crabs are not obvious. Habitat heterogeneity is an obvious cause of aggregation in some species, especially mobile ones (Brown and Orians, 1970; Poole, 1974). Species

tend to aggregate in areas providing adequate resources and optimal conditions. Environmental variables measured during this study did not appear to differ enough within habitat types to account for the podding behavior. For example, water temperature and salinity did not differ significantly at adjacent areas of the shallowwater habitat, yet aggregations utilized only a small percentage of the habitat available to them. Similarly, aggregations formed only within well defined areas, while adjacent, seemingly identical habitats were seldom utilized.

If the clumping of individuals is greater than would be expected on the basis of resource patchiness alone, their distribution (home range) may be influenced by the presence of conspecifics (Brown and Orians, 1970). Excluding aggregations near clumped resources, Brown and Orians (1970) identify four functions which could be enhanced by associations of individuals: 1) group defense against predators; 2) group defense of feeding areas; 3) the ability to exploit resources more readily than solitary individuals; and 4) the ability to profit from the foraging success of other individuals by observing where they find food. Although detailed in situ observations of red king crab feeding behavior are lacking, they are considered to be extremely opportunistic predators/scavengers (Jewett and Feder, 1982). As such, their foraging success is probably not significantly enhanced by group behavior. The latter three functions may be enhanced by group association, but none are likely the primary motive of aggregating behavior in red king crabs. Group defense against predators (i.e., earlier predator detection via increased

vigilance of larger groups (Magurran, 1990)), however, is one possible effective function of podding behavior in red king crabs.

Juvenile red king crab are thought to form pods mainly as a protective measure (Powell and Nickerson, 1965b; Powell, 1972; Somerton, 1985). Dew (1990) attributes the inception of podding behavior in juveniles to decreased refuge availability as crabs grow larger. He further suggests podding in juveniles as a strategy to avoid detection by a diurnally active predator; podding is more typical during the day.

Whether podding also serves as a behavioral defense mechanism in adult red king crabs is unknown. The giant Pacific octopus, *Octopus dofleini,* is probably the only important shallowwater predator of adult red king crabs. An ultrasonic tag attached to a primiparous female in spring 1989 was found at a depth of 15 m near the entrance to an occupied octopus den. Although podding behavior would not completely eliminate the threat of octopus predation, individuals would increase their fitness according to the "selfish herd" hypothesis (Hamilton, 1971). According to this hypothesis, gregarious behavior is considered a selfish cover-seeking instinct of individuals; they attempt to put conspecifics between themselves and potential predators (Hamilton, 1971).

Podding behavior has also been reported for several other large adult crustaceans. Dense aggregations of the spiny lobster, *Panulirus argus*, have been observed to form for the purposes of migrating (Berrill, 1975). Campbell (1990)

attributed the clumped distribution of berried female American lobsters, *Homarus americanus*, to selection of preferred habitats for egg development and larval dispersal. Podding behavior has been noted in three species of spider crabs, and has been suggested as a protective mechanism during molting and mating (Carlisle, 1957; Ševčić, 1971; DeGoursey and Stewart, 1985; Hanauer, 1988).

Dense aggregations of adult red king crabs have only been reported during late winter and early spring and are also thought to form strictly for the purpose of molting and mating (Powell and Nickerson, 1965a). Female red king crabs in this study began to form dense aggregations as early as November after migrating to shallow water. Male crabs, however, were not observed in association with these aggregations until late January, and molting and mating was not observed until early March. Although some degree of aggregation certainly exists after March, when crabs seemed to disband somewhat and migrate to intermediate depths, clasping pairs were generally solitary in shallowwater areas. Clasping pairs often utilized macrophytes and reef-type complexes as cover, but only remained in shallowwater areas for a brief period following mating. Molting and mating was occasionally observed near aggregations, but only near the periphery, never within aggregations, as has been reported for other species (Carlisle, 1957; Ševčić, 1971; DeGoursey and Stewart, 1985; Hanauer, 1988). Formation of dense aggregations might serve to concentrate females near spawning areas, increasing the frequency of male-female encounters, and consequently improving mating opportunities.

A similar purpose for shallowwater aggregations of Dungeness crabs (*Cancer magister*) has been reported (Butler, 1960).

Shallowwater observations by SCUBA and movement data from ultrasonic tracking suggest that females are generally inactive during the winter months. Water temperatures during this period were greatly reduced in shallowwater areas, and probably significantly lowered the metabolic requirements of the crabs. All diving and tracking operations were conducted during daylight hours, however. Whether adults form these aggregations during daylight hours and become more active disbanding into loosely-knit feeding groups at night is unknown. Dew (1990) observed such a daily activity pattern for juvenile crabs.

Although the distribution and movements of crabs tagged and released in May and June 1989 were monitored only periodically, the patterns of seasonal distribution for these crabs and those monitored weekly from May/June 1988 to May 1989 were remarkably similar. Furthermore, diver observations confirmed that tagged crabs formed dense aggregations in the same areas during both years. These data suggest that podding behavior may be an annual event for adult female red king crabs and that there may be little interannual variation in the areas where these aggregations form.

Gregarious behavior is an adaptation which has been selected in the course of evolution because it enhances an individual's ability to compete for the requisites for reproduction and survival (Brown and Orians, 1970). Podding is

likely an integral behavioral adaptation of juvenile red king crabs, that is periodically observed in adults. The direct function that podding serves in adults remains unknown, although the preservation of this highly organized, inherent behavior likely serves to organize the population into subgroups for the purposes of molting and mating during late winter and spring. The degree of gregariousness and factors influencing this behavior in adults probably changes seasonally in response to the spatial and temporal distribution of resources. The apparent shift in degree of aggregation observed seasonally may directly indicate spatial differences in resource patchiness. Selfish cover-seeking, as a means of predator defense, may likely play an important role during winter when crabs occupy shallow water.

The question of why adult red king crabs aggregate is an important one. Hamilton (1971) suggests that cooperative relationships and some degree of social hierarchy may be common amongst species that aggregate. Little is known regarding the social behavior of red king crabs and the presence of altruistic or agonistic behavior. Future work should concentrate on the factors influencing the aggregative behavior of red king crabs.

Collection of detailed in situ observations of red king crab aggregations should continue to provide information concerning behavioral responses to spatial and temporal changes in resource patchiness. Unfortunately, hypothesis-testing protocols in the field are often unattainable due to logistical limitations.

Hypotheses concerning the reasons for podding behavior in red king crabs could be tested in an enclosed experimental facility, however. The facility should be sufficiently large to mimic natural conditions. The "selfish herd" hypothesis could be tested in such a facility by introducing predators, and monitoring the crabs' behavior. The resources available to the test animals could be manipulated to determine if spatial or temporal changes in resources result in behavioral adaptations. The relationship between life history events (molting and mating) and podding behavior could also be monitored in detail in such a facility.

CHAPTER IV.

CONCLUSIONS

This study represents an extensive documentation of long-term movements and seasonal distribution of a large, commercially important crustacean. In addition, this study provides the first detailed documentation of "podding" behavior in adult red king crabs.

The migrations undertaken by female red king crabs were associated with life history events and may have occurred in response to spatial and temporal variations in environmental conditions and resources. These movements were probably seasonally dependent and consisted of three separate major events. Females gradually migrated to depth in late spring after molting and mating had occurred. They remained in deepwater areas during summer and fall actively foraging in loose aggregations. Crabs occupied areas below a well-developed thermocline where environmental conditions were relatively stable.

Crabs moved abruptly into shallow water in November following fall thermohaline mixing. This highly synchronized movement of crabs was coincident with the decay of the thermocline/halocline and may have been ultimately triggered by decreasing photoperiod. The water column was well-mixed and essentially homogeneous with respect to temperature and salinity during this period. Crabs may have moved into shallowwater areas during winter to take

advantage of the increased benthic production. Crabs were generally highly aggregated during winter and exhibited "podding" behavior previously documented only for juveniles. "Podding" behavior might serve as a defense mechanism against shallowwater predators and might serve to organize the population into subgroups in late winter when mating activity begins. Optimum shallowwater habitats may typically be less abundant than deepwater habitat and further augment the tendency to aggregate during winter.

Crabs gradually, but synchronously, moved to intermediate depths in March when the thermocline and halocline began to redevelop. In doing so, females probably avoided the developing unfavorable conditions in shallow water. Eggs attached to the females' pleopods probably hatched before they moved back into shallow water in April and May to molt and mate.

Seasonal movements were generally similar for primiparous and multiparous females. Primiparous crabs molted and mated earlier than multiparous females, and consequently began their migration into shallow water earlier in spring. In general, movements of multiparous crabs were more conservative and consistent than those of primiparous crabs. The relatively inconsistent behavior displayed by primiparous crabs might result from the ontogenetic changes associated with maturity.

The relatively small home ranges and great fidelity to spring spawning areas reported for female red king crabs in this thesis, especially multiparous females,

may indicate that crabs constitute localized stocks. Male red king crabs may also have restricted ranges and constitute resident populations (unpublished data). Bays not widely separated within Southeast Alaska may support genetically separate stocks of red king crab (Seeb and Seeb, 1987). Knowledge of the migratory behavior of red king crab is essential for an understanding of king crab stock relationships and population dynamics. These data may be of particular importance in areas in Southeast Alaska, since small localized populations of red king crab would be especially vulnerable to poor management practices.

Surveys of red king crab have been conducted by the Alaska Department of Fish and Game (Division of Commercial Fisheries) annually since 1979 in Southeast Alaska, despite the fact that this fishery has been closed since 1985. The main objectives of these surveys were to estimate relative abundance and stock composition of red king crabs interannually and use this information to develop fishery management plans. Seasonal shifts in habitat use by red king crabs and their gregarious behavior may greatly complicate estimates of relative abundance and stock composition, however. This study provides new information concerning seasonal migration and distribution of red king crabs. If seasonal movements and distribution of female red king crabs in Auke Bay are generally indicative of those elsewhere, then survey efforts could be adjusted, both temporally and spatially, to provide the most accurate estimates.

Additional long-term data are essential to determine if seasonal migrations and distribution of female red king crabs are stable interannually (i.e., are they predictable from year to year). Laboratory studies of physiology and behavior in conjunction with continued monitoring of environmental conditions should be undertaken to determine the underlying mechanisms of these movements. Finally, similar research should be undertaken with male red king crabs to determine if they also have restricted movements and potentially comprise localized stocks.

Appendix 1. Tracking record for crab No. 249 (see map on page 103).

Sequence No.	Date	Depth (m)	Distance (m)
0	5/17/88	19.8	—
1	5/23/88	57.6	778.8
2	6/05/88	79.6	1183.3
3	7/26/88	81.1	5554.9
4	8/01/88	116.1	959.2
5	8/09/88	89.3	1632.4
6	8/15/88	106.7	540.8
7	8/22/88	97.2	569.7
8	8/30/88	96.6	176.0
9	9/06/88	95.7	94.4
10	9/13/88	104.9	348.0
11	9/22/88	65.2	342.6
12	9/30/88	66.8	856.7
13	10/11/88	69.8	663.4
14	10/19/88	79.9	1007.9
15	10/25/88	46.0	939.7
16	11/04/88	37.2	223.1
17	11/11/88	61.0	387.5
18	11/16/88	40.2	233.8
19	12/01/88	24.4	236.0
20	1/05/89	17.7	269.9
21	1/26/89	9.1	161.1
22	2/07/89	55.2	585.5
23	3/13/89	14.3	5440.3
24	3/24/89	20.4	504.0
25	4/06/89	17.7	14.0
26	4/11/89	8.2	99.3
27	4/19/89	14.3	344.4
28	4/25/89	16.5	16.2
29	5/03/89	28.4	268.8
30	*5/10/89	31.4	105.8

* The tag remained stationary hereafter indicating that the crab probably molted at depth sometime prior to this date.

Appendix 2. Tracking record for crab No. 267 (see map on page 104).

Sequence No.	Date	Depth (m)	Distance (m)
0	5/17/88	19.8	—
1	5/24/88	59.1	950.6
2	6/01/88	59.4	708.9
3	6/05/88	39.9	1001.5
4	6/20/88	59.7	352.8
5	6/27/88	65.8	118.5
6	7/05/88	60.4	219.8
7	7/13/88	54.0	178.1
8	7/19/88	90.2	723.3
9	7/27/88	51.5	1004.7
10	8/01/88	59.1	418.5
11	8/09/88	52.1	359.4
12	8/15/88	50.9	100.0
13	8/23/88	52.4	89.5
14	8/30/88	53.0	30.5
15	9/07/88	63.7	544.0
16	9/14/88	72.9	1015.9
17	9/23/88	48.5	2419.2
18	9/27/88	50.0	703.7
19	10/12/88	48.5	192.6
20	10/20/88	50.3	191.0
21	10/26/88	51.8	155.0
22	11/03/88	47.2	638.0
23	11/11/88	51.8	509.2
24	11/18/88	52.7	235.5
25	12/01/88	87.8	2460.0
26	12/12/88	54.6	786.9
27	1/12/89	15.9	408.3
28	1/26/89	9.5	369.2
29	2/07/89	11.3	199.5
30	2/22/89	8.5	259.6
31	3/06/89	19.5	225.0
32	3/14/89	53.0	327.8
33	3/30/89	16.2	313.6
34	4/05/89	36.3	2982.0
35	4/12/89	35.7	137.9
36	4/18/89	8.8	508.9
37	*4/19/89	7.6	227.2

* The crab was retrieved by divers and molted in the laboratory on 4/22/89.

Appendix 3. Tracking record for crab No. 339 (see map on page 105).

Sequence No.	Date	Depth (m)	Distance (m)
0	5/17/88	19.8	—
1	6/01/88	52.1	266.7
2	*6/27/88	14.6	147.0

* The tag was recovered by divers in shallow water and appeared to have been torn free of the crab's carapace.

Appendix 4. Tracking record for crab No. 339A (see map on page 106).

Sequence No.	Date	Depth (m)	Distance (m)
0	8/01/88	26.5	—
1	8/09/88	56.7	478.9
2	8/15/88	56.1	165.1
3	8/23/88	64.9	835.1
4	8/30/88	65.8	282.5
5	9/07/88	63.4	38.5
6	9/14/88	71.3	612.4
7	9/23/88	48.8	3238.4
8	9/27/88	48.8	303.7
9	10/12/88	45.7	306.1
10	10/20/88	45.4	147.8
11	10/26/88	44.8	284.1
12	11/04/88	44.5	233.4
13	11/11/88	46.3	194.8
14	11/18/88	18.6	2143.7
15	12/02/88	23.5	735.0
16	12/13/88	8.5	283.1
17	1/06/89	11.0	255.2
18	1/13/89	11.6	478.1
19	2/07/89	19.5	417.0
20	2/23/89	24.7	2177.0
21	3/07/89	40.8	447.9
22	3/14/89	43.9	345.4
23	*3/30/89	43.3	183.8

* The tag remained stationary after this date due to unknown reasons.

Appendix 5. Tracking record for crab No. 348 (see map on page 107).

Sequence No.	Date	Depth (m)	Distance (m)
0	5/17/88	19.8	—
1	5/23/88	49.1	356.4
2	6/01/88	54.0	134.0
3	6/20/88	33.2	159.1
4	6/27/88	56.4	293.8
5	7/05/88	75.3	746.3
6	7/11/88	59.1	723.1
7	7/26/88	98.5	3215.9
8	8/01/88	96.6	245.9
9	8/09/88	87.2	1072.1
10	8/15/88	89.3	827.5
11	8/22/88	90.8	209.6
12	8/30/88	90.2	277.6
13	9/06/88	70.7	925.1
14	9/13/88	68.3	416.0
15	9/22/88	52.7	367.2
16	9/30/88	56.4	270.5
17	10/11/88	38.4	982.0
18	10/19/88	47.6	297.2
19	10/25/88	59.1	729.0
20	11/04/88	57.6	482.5
21	11/10/88	45.4	1067.0
22	11/16/88	7.9	453.2
23	12/01/88	8.5	66.0
24	12/12/88	11.6	22.6
25	1/05/89	32.6	387.9
26	1/26/89	24.4	2426.9
27	2/07/89	15.9	1312.5
28	2/22/89	21.6	3289.5
29	3/06/89	33.5	1254.6
30	3/13/89	18.6	704.5
31	3/30/89	50.3	348.8
32	4/05/89	48.2	108.5
33	4/11/89	55.8	628.0
34	4/18/89	39.6	1093.7
35	4/26/89	27.7	241.7
36	*5/03/89	36.6	328.0

* The tag remained stationary hereafter indicating that the crab probably molted at depth sometime prior to this date.

Appendix 6. Tracking record for crab No. 357 (see map on page 108).

Sequence No.	Date	Depth (m)	Distance (m)
0	5/17/88	19.8	—
1	5/23/88	48.8	379.5
2	6/20/88	33.2	249.6
3	6/27/88	54.0	131.3
4	7/05/88	32.3	190.4
5	7/11/88	46.6	490.8
6	7/19/88	73.8	582.6
7	7/26/88	98.5	2944.2
8	8/03/88	87.5	873.6
9	8/09/88	82.3	1384.1
10	8/15/88	78.9	1192.6
11	8/22/88	111.3	449.5
12	8/30/88	95.7	647.9
13	9/06/88	100.6	304.3
14	9/13/88	105.5	143.3
15	9/22/88	67.1	331.7
16	9/30/88	77.7	1115.1
17	10/11/88	69.8	834.2
18	10/19/88	76.2	1025.6
19	10/25/88	46.0	930.7
20	11/04/88	37.2	223.1
21	11/10/88	61.0	387.5
22	11/16/88	35.7	364.4
23	12/01/88	24.4	142.8
24	12/12/88	36.3	409.4
25	1/05/89	32.6	1100.8
26	1/26/89	24.4	2426.9
27	2/07/89	15.9	1312.5
28	2/22/89	21.6	3289.4
29	3/06/89	16.8	835.1
30	3/13/89	17.1	44.6
31	3/30/89	22.3	241.3
32	4/05/89	17.4	464.8
33	*4/10/89	7.3	89.5

* The crab was retrieved by divers and died of apparent molt stress in the laboratory on 4/20/89.

Appendix 7. Tracking record for crab No. 366 (see map on page 109).

Sequence No.	Date	Depth (m)	Distance (m)
0	5/17/88	19.8	—
1	5/20/88	37.5	177.4
2	5/23/88	48.5	181.9
3	6/01/88	39.3	231.4
4	6/27/88	51.5	453.6
5	7/05/88	62.2	408.1
6	7/11/88	68.9	668.8
7	7/19/88	68.0	48.2
8	7/27/88	88.1	585.0
9	8/01/88	58.8	1553.7
10	8/09/88	53.7	1495.0
11	*8/10/88	42.1	—
12	8/16/88	47.6	665.1
13	8/24/88	50.3	698.9
14	9/01/88	46.6	1096.4
15	9/08/88	46.3	1218.1
16	9/14/88	46.6	527.6
17	9/23/88	49.1	294.6
18	9/27/88	50.9	607.3
19	10/12/88	46.3	515.0
20	10/20/88	50.0	510.1
21	10/26/88	49.4	160.6
22	11/03/88	46.0	482.6
23	11/11/88	43.9	1036.6
24	11/18/88	32.6	647.8
25	12/02/88	37.2	224.9
26	12/13/88	41.5	182.2
27	1/06/89	37.5	144.8
28	1/13/89	16.2	376.4
29	2/07/89	15.5	336.3
30	2/23/89	31.4	1844.5
31	3/07/89	42.7	190.9
32	3/14/89	45.1	1073.5
33	3/30/89	40.2	1289.4
34	4/06/89	43.0	634.4
35	4/12/89	45.7	1737.6
36	4/18/89	56.4	315.3
37	4/26/89	69.2	1043.4
38	5/03/89	26.8	665.9
39	5/04/89	60.7	649.3
40	5/10/89	62.8	393.5
41	†5/17/89	61.6	190.8

* Release of crab after being caught in a sport pot on 8/09/88.

† The tag remained stationary hereafter indicating that the crab probably molted at depth sometime prior to this date.

Appendix 8. Tracking record for crab No. 375 (see map on page 110).

Sequence No.	Date	Depth (m)	Distance (m)
0	5/17/88	19.8	—
1	5/23/88	52.4	539.9
2	6/01/88	61.6	147.5
3	6/20/88	39.0	519.3
4	6/27/88	56.4	445.1
5	7/05/88	57.3	332.9
6	*7/11/88	56.1	146.8

* The tag remained stationary after this date due to unknown reasons.

Appendix 9. Tracking record for crab No. 384 (see map on page 111).

Sequence No.	Date	Depth (m)	Distance (m)
0	5/17/88	19.8	—
1	5/24/88	50.3	382.1
2	6/01/88	59.4	315.2
3	6/27/88	45.7	335.8
4	7/05/88	56.4	928.7
5	7/13/88	54.0	39.2
6	7/21/88	53.7	14.6
7	8/01/88	55.5	36.7
8	8/09/88	86.9	1134.8
9	8/15/88	77.4	2346.2
10	8/22/88	83.5	1575.4
11	8/30/88	79.2	720.3
12	9/06/88	47.9	1032.4
13	9/13/88	33.2	161.7
14	9/22/88	50.9	94.8
15	9/30/88	56.4	275.8
16	10/11/88	38.4	982.0
17	10/19/88	47.6	297.2
18	10/25/88	59.1	661.5
19	11/04/88	69.2	1281.7
20	11/10/88	55.5	106.1
21	11/16/88	35.7	322.0
22	12/01/88	24.4	142.8
23	12/12/88	36.3	409.4
24	1/05/89	17.7	472.8
25	1/26/89	9.1	161.1
26	2/07/89	47.6	272.8
27	2/22/89	17.4	267.0
28	3/06/89	10.7	88.4
29	3/13/89	18.0	301.8
30	3/24/89	67.4	638.1
31	4/05/89	19.2	761.2
32	4/11/89	14.0	244.2
33	4/18/89	7.9	235.8
34	*4/20/89	12.5	199.8

* The crab was retrieved by divers and molted in the laboratory on 4/23/89.

Appendix 10. Tracking record for crab No. 447 (see map on page 112).

Sequence No.	Date	Depth (m)	Distance (m)
0	5/17/88	19.8	—
1	5/20/88	53.0	869.0
2	5/24/88	51.8	302.9
3	6/05/88	85.0	1246.1
4	6/20/88	52.7	781.9
5	6/28/88	51.8	391.3
6	7/06/88	51.8	143.9
7	7/13/88	52.4	102.1
8	7/21/88	86.6	1151.5
9	7/27/88	52.1	1095.7
10	8/01/88	45.4	200.0
11	8/09/88	43.0	26.6
12	8/15/88	38.7	28.2
13	8/23/88	56.4	542.2
14	8/30/88	54.0	49.2
15	9/08/88	42.1	3367.2
16	9/14/88	44.5	498.8
17	9/23/88	44.8	1210.1
18	9/27/88	46.3	215.1
19	10/12/88	46.3	134.1
20	10/20/88	50.0	428.3
21	10/26/88	49.1	207.5
22	11/03/88	47.6	316.5
23	11/11/88	50.0	403.9
24	11/18/88	26.5	1175.6
25	12/02/88	37.2	296.1
26	12/13/88	32.0	220.4
27	1/06/89	36.0	134.6
28	1/13/89	51.2	1136.7
29	2/07/89	35.1	1809.8
30	2/23/89	24.4	289.3
31	3/07/89	36.3	285.5
32	3/14/89	40.2	597.5
33	3/30/89	35.1	619.2
34	4/05/89	34.1	126.6
35	4/12/89	32.6	95.4
36	4/19/89	37.8	227.2
37	*5/10/89	40.5	6539.3

* The tag remained stationary hereafter indicating that the crab probably molted at depth sometime prior to this date.

Appendix 11. Tracking record for crab No. 456 (see map on page 113).

Sequence No.	Date	Depth (m)	Distance (m)
0	5/17/88	19.8	—
1	5/24/88	55.8	308.6
2	6/05/88	54.3	743.4
3	6/20/88	58.5	663.0
4	6/28/88	53.7	624.3
5	7/05/88	80.0	1587.8
6	7/13/88	64.9	847.9
7	7/19/88	77.7	2965.7
8	7/26/88	98.2	1333.4
9	8/01/88	84.1	270.9
10	8/15/88	37.5	3494.7
11	8/23/88	45.4	231.6
12	*8/30/88	54.9	243.6

* Last date this tag could be isolated within the study area.

Appendix 12. Tracking record for crab No. 2228 (see map on page 114).

Sequence No.	Date	Depth (m)	Distance (m)
0	6/03/88	16.2	—
1	6/14/88	46.0	904.7
2	*6/24/88	46.6	306.4

* The tag remained stationary after this date due to unknown reasons.

Appendix 13. Tracking record for crab No. 2237 (see map on page 115).

Sequence No.	Date	Depth (m)	Distance (m)
0	6/03/88	16.2	—
1	6/21/88	33.2	378.1
2	6/29/88	33.2	2.8
3	7/06/88	33.5	61.1
4	7/13/88	34.8	89.4
5	7/26/88	34.1	22.0
6	8/03/88	37.8	245.5
7	8/11/88	36.0	99.6
8	8/16/88	36.3	143.4
9	8/24/88	33.2	62.7
10	9/01/88	36.3	99.1
11	9/07/88	32.3	165.8
12	9/14/88	45.7	2161.4
13	9/23/88	45.7	792.6
14	9/27/88	45.1	182.4
15	10/12/88	46.3	472.2
16	10/19/88	48.5	253.9
17	10/26/88	45.4	503.5
18	11/04/88	44.2	232.6
19	11/11/88	49.1	784.5
20	11/18/88	18.6	1659.4
21	12/02/88	23.5	735.0
22	12/13/88	8.5	283.1
23	1/06/89	11.0	255.2
24	1/13/89	11.6	478.1
25	2/07/89	28.0	2627.0
26	2/23/89	37.5	1103.0
27	3/07/89	43.0	403.6
28	3/14/89	43.6	73.1
29	3/30/89	38.4	1012.4
30	4/05/89	33.0	451.7
31	4/12/89	26.2	28.8
32	4/14/89	22.9	418.9
33	4/19/89	32.3	53.9
34	4/26/89	38.1	43.9
35	5/04/89	39.6	179.4
36	5/11/89	43.0	335.4
37	5/18/89	34.8	377.2
38	5/21/89	43.3	379.0
39	*5/24/89	24.1	415.3

* The crab was retrieved by divers and died of apparent molt stress on 5/27/89.

Appendix 14. Tracking record for crab No. 2246 (see map on page 116).

Sequence No.	Date	Depth (m)	Distance (m)
0	6/03/88	16.2	—
1	6/14/88	47.2	950.8
2	6/21/88	50.0	1161.4
3	6/29/88	43.9	822.6
4	7/06/88	33.5	925.0
5	7/13/88	30.2	86.9
6	7/26/88	33.5	58.3
7	8/02/88	33.5	3.8
8	8/11/88	35.1	228.3
9	8/16/88	45.1	1340.7
10	8/25/88	51.8	843.2
11	9/01/88	45.7	1116.6
12	9/08/88	44.5	664.8
13	9/14/88	44.2	185.2
14	9/23/88	43.6	29.0
15	9/27/88	44.8	71.5
16	10/12/88	44.2	147.1
17	10/19/88	43.0	51.9
18	10/26/88	41.2	678.1
19	11/04/88	31.4	750.4
20	11/11/88	45.1	1567.8
21	11/18/88	29.3	1708.6
22	12/02/88	32.3	127.3
23	12/12/88	35.4	92.6
24	1/06/89	29.9	317.9
25	1/13/89	32.6	71.3
26	2/07/89	50.0	2479.2
27	*2/22/89	48.2	249.0

* The tag remained stationary after this date due to unknown reasons.

Appendix 15. Tracking record for crab No. 2255 (see map on page 117).

Sequence No.	Date	Depth (m)	Distance (m)
0	6/03/88	16.2	—
1	6/21/88	43.9	1500.8
2	6/29/88	39.3	620.5
3	7/06/88	33.5	2007.3
4	7/13/88	33.2	60.7
5	7/26/88	35.1	288.0
6	8/02/88	38.1	290.9
7	8/11/88	35.1	270.7
8	8/16/88	46.9	1497.9
9	8/24/88	47.2	272.0
10	9/01/88	44.2	317.8
11	9/08/88	46.0	291.0
12	9/14/88	45.1	119.1
13	9/23/88	45.4	147.7
14	9/27/88	45.1	51.4
15	10/12/88	45.4	131.7
16	10/20/88	44.2	636.6
17	10/26/88	45.4	385.3
18	11/03/88	45.7	770.5
19	11/11/88	45.4	233.4
20	11/18/88	43.3	540.8
21	12/02/88	23.8	452.1
22	12/13/88	46.6	372.8
23	1/06/89	11.0	1545.6
24	1/13/89	11.6	478.1
25	2/07/89	19.8	417.0
26	2/23/89	33.2	2229.6
27	3/07/89	46.0	1037.0
28	3/14/89	39.6	1026.7
29	3/30/89	39.9	362.8
30	4/06/89	37.8	167.6
31	4/12/89	18.9	23.7
32	4/19/89	14.6	259.3
33	4/26/89	36.9	436.9
34	5/04/89	38.1	305.6
35	5/11/89	40.2	85.0
36	5/18/89	44.2	389.1
37	5/21/89	43.6	148.8
38	5/24/89	43.3	250.4
39	5/25/89	41.5	372.4
40	5/26/89	41.5	262.8
41	5/29/90	30.5	1170.8
42	*5/30/89	22.9	202.3

* The crab was retrieved by divers and molted in the laboratory on 5/31/90.

Appendix 16. Tracking record for crab No. 258 (see map on page 118).

Sequence No.	Date	Depth (m)	Distance (m)
0	6/03/88	16.2	—
1	6/21/88	47.9	1583.5
2	6/29/88	46.9	476.1
3	7/06/88	46.0	1531.4
4	7/13/88	55.8	1347.3
5	7/26/88	47.2	1206.7
6	8/02/88	47.6	220.5
7	8/10/88	45.7	226.2
8	8/16/88	46.0	196.7
9	8/23/88	48.8	318.4
10	9/01/88	48.5	197.3
11	9/08/88	46.6	268.2
12	9/14/88	45.4	193.4
13	9/23/88	47.9	353.0
14	9/27/88	50.3	271.0
15	10/12/88	45.4	368.1
16	10/19/88	54.3	434.5
17	10/26/88	48.8	609.3
18	11/03/88	47.9	295.2
19	11/11/88	50.0	223.3
20	11/18/88	18.6	1212.1
21	12/02/88	23.5	735.0
22	12/13/88	8.5	283.1
23	1/06/89	11.0	255.2
24	1/13/89	11.6	478.1
25	2/07/89	19.5	417.0
26	2/23/89	39.9	2150.8
27	3/14/89	44.5	1614.7
28	3/30/89	40.4	1330.8
29	4/06/89	38.1	260.8
30	4/12/89	36.9	359.0
31	4/19/89	38.7	85.9
32	4/26/89	38.4	152.6
33	5/04/89	39.3	172.8
34	5/11/89	42.4	304.2
35	*5/16/89	22.9	560.9

* The crab was recovered by divers and had attempted to molt during the previous 24 hours but was unsuccessful due to the attachment of the tag harness.

Appendix 17. Tracking record for crab No. 276 (see map on page 119).

Sequence No.	Date	Depth (m)	Distance (m)
0	6/03/88	16.2	—
1	6/14/88	46.3	897.9
2	7/06/88	46.9	1204.3
3	7/13/88	46.9	40.5
4	7/21/88	47.2	192.8
5	7/26/88	50.0	317.9
6	8/02/88	50.3	1124.1
7	8/10/88	48.8	105.3
8	8/16/88	47.6	157.4
9	8/25/88	50.6	285.4
10	9/01/88	48.2	274.5
11	9/08/88	47.9	169.8
12	9/14/88	44.2	355.7
13	9/23/88	45.4	210.0
14	9/27/88	45.7	85.5
15	10/12/88	46.3	190.6
16	10/20/88	46.3	184.1
17	10/26/88	45.7	425.9
18	11/04/88	47.9	255.0
19	11/11/88	45.4	64.4
20	11/18/88	48.5	584.7
21	12/02/88	36.0	1118.1
22	12/13/88	50.3	694.8
23	1/06/89	40.8	368.7
24	1/13/89	43.9	286.5
25	2/07/89	44.5	56.5
26	2/22/89	62.5	1271.7
27	3/07/89	46.0	1946.3
28	3/14/89	40.2	960.6
29	3/30/89	42.7	281.0
30	4/05/89	38.1	419.9
31	4/12/89	37.5	90.4
32	4/19/89	37.5	21.3
33	4/26/89	37.8	7.2
34	5/04/89	40.2	347.6
35	5/11/89	42.4	338.5
36	5/18/89	44.8	307.1
37	5/21/89	45.4	328.8
38	*5/24/89	23.8	1319.1

* The crab was retrieved by divers and molted in the laboratory on 5/28/89.

Appendix 18. Tracking record for crab No. 285 (see map on page 120).

Sequence No.	Date	Depth (m)	Distance (m)
0	6/03/88	16.2	—
1	6/14/88	46.9	1060.4
2	6/24/88	45.4	278.9
3	6/29/88	47.9	355.3
4	7/06/88	48.5	218.0
5	7/21/88	54.6	2964.8
6	7/26/88	47.2	2447.2
7	8/03/88	43.3	1573.4
8	8/10/88	41.8	401.3
9	8/16/88	43.6	180.2
10	8/24/88	40.8	290.1
11	9/01/88	33.8	462.7
12	9/07/88	33.5	3.4
13	9/14/88	43.9	1778.0
14	9/22/88	53.7	1567.5
15	10/12/88	43.6	2020.0
16	10/20/88	49.1	911.9
17	*10/26/88	43.3	774.1

* The tag remained stationary after this date due to unknown reasons.

Appendix 19. Tracking record for crab No. 294 (see map on page 121).

Sequence No.	Date	Depth (m)	Distance (m)
0	6/03/88	16.2	—
1	6/14/88	32.0	356.3
2	6/21/88	33.2	100.5
3	6/29/88	32.9	14.8
4	7/06/88	33.5	77.4
5	7/13/88	32.3	19.6
6	7/27/88	35.4	142.3
7	8/02/88	44.8	1199.1
8	8/10/88	45.1	407.0
9	8/16/88	35.1	898.5
10	8/24/88	34.1	134.7
11	9/01/88	46.9	1667.8
12	9/08/88	46.0	542.1
13	9/14/88	44.8	256.5
14	9/23/88	44.8	181.0
15	9/27/88	44.8	454.6
16	10/12/88	46.6	1040.6
17	10/19/88	37.2	2190.1
18	10/26/88	34.4	157.3
19	11/04/88	48.2	2153.0
20	11/11/88	41.5	682.2
21	11/18/88	5.5	721.6
22	12/01/88	7.6	17.5
23	12/13/88	8.5	852.4
24	1/06/89	11.0	255.2
25	1/13/89	11.6	478.1
26	2/07/89	19.5	417.0
27	2/23/89	34.1	2183.8
28	3/07/89	45.1	1462.0
29	3/14/89	37.2	1790.9
30	*3/30/89	36.6	318.5

* The tag was received in an anonymous package with a note indicating that the crab had been caught on 3/31/89. The fate of the crab is unknown.

Appendix 20. Tracking record for crab No. 465 (see map on page 122).

Sequence No.	Date	Depth (m)	Distance (m)
0	6/03/88	16.2	—
1	6/14/88	24.7	1179.2
2	*6/21/88	26.2	138.5

* Divers recovered the tag and intact attachment cable in shallow water. Because the cable and attached tag could not have slipped off the crab intact, the crab was probably the victim of predation or illegal harvest.

Appendix 21. Tracking record for crab No. 465A (see map on page 123).

Sequence No.	Date	Depth (m)	Distance (m)
0	8/01/88	28.4	—
1	8/10/88	46.9	619.5
2	8/16/88	47.2	387.2
3	8/24/88	46.9	561.0
4	9/01/88	46.9	1319.4
5	9/07/88	44.2	248.2
6	9/14/88	44.8	1559.3
7	9/23/88	46.9	306.8
8	9/27/88	47.2	238.0
9	10/12/88	44.8	202.0
10	10/20/88	44.8	181.6
11	10/26/88	46.3	472.0
12	11/03/88	47.6	1041.7
13	11/10/88	52.7	663.7
14	11/18/88	18.6	1281.2
15	12/02/88	23.5	735.0
16	12/13/88	8.5	283.1
17	1/06/89	11.0	255.2
18	1/13/89	11.6	478.1
19	2/07/89	19.5	417.0
20	2/22/89	53.7	709.9
21	3/14/89	33.2	1534.6
22	3/30/89	18.3	292.1
23	4/06/89	21.3	212.8
24	4/12/89	20.4	91.1
25	4/19/89	18.0	52.2
26	4/27/89	19.2	365.6
27	5/04/89	22.6	180.3
28	5/11/89	25.0	127.3
29	*5/17/89	4.3	658.4

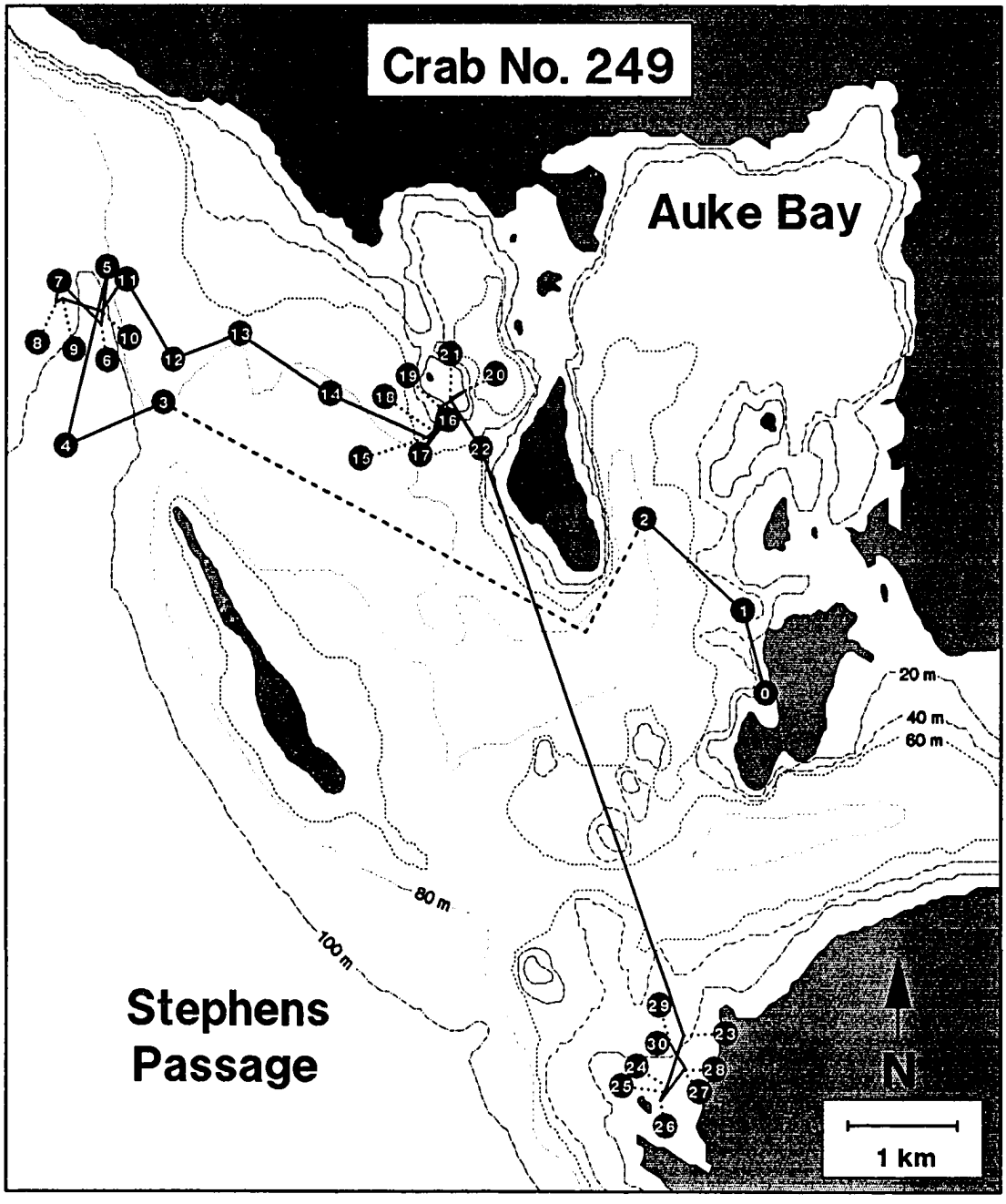
* The crab was retrieved by divers and molted in the laboratory on 5/20/89.

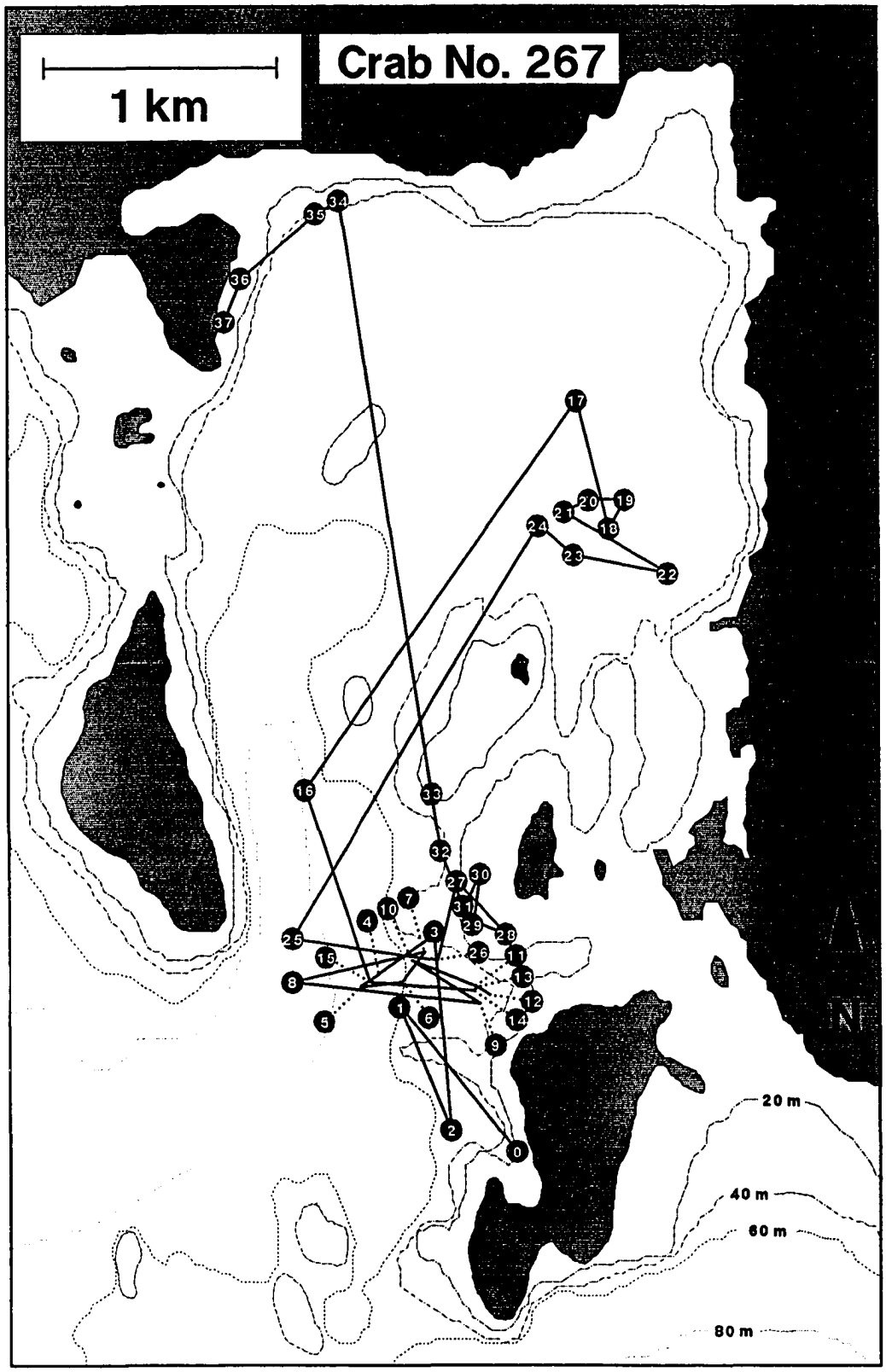
Appendix 22. Tracking record for crab No. 555 (see map on page 124).

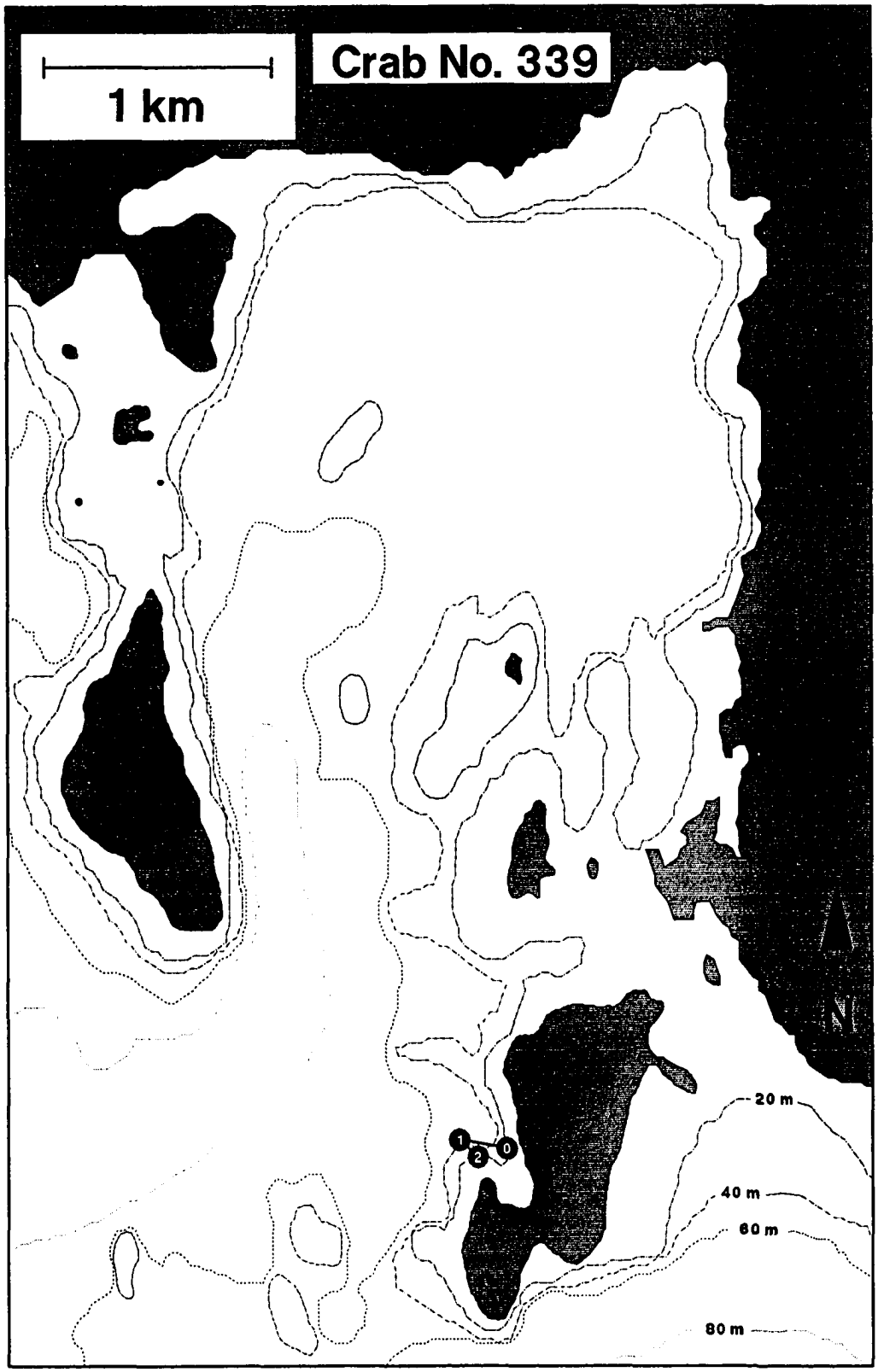
Sequence No.	Date	Depth (m)	Distance (m)
0	6/03/88	16.2	—
1	6/14/88	44.8	871.7
2	6/24/88	43.0	270.4
3	6/29/88	43.9	216.6
4	7/06/88	44.5	208.4
5	7/13/88	43.6	82.8
6	7/26/88	46.0	1338.8
7	8/02/88	46.6	101.6
8	8/10/88	45.7	178.5
9	8/16/88	45.1	89.1
10	8/25/88	45.4	204.2
11	9/01/88	45.4	23.3
12	9/08/88	44.5	58.4
13	9/14/88	44.8	59.4
14	9/23/88	44.5	438.1
15	9/27/88	44.5	28.8
16	10/12/88	45.4	119.1
17	10/20/88	49.7	502.0
18	11/03/88	46.6	384.2
19	11/10/88	54.9	1122.1
20	11/18/88	25.9	1509.8
21	12/02/88	35.7	315.9
22	12/12/88	33.5	125.6
23	1/06/89	11.0	376.2
24	1/13/89	11.6	478.1
25	2/07/89	19.5	417.0
26	2/23/89	42.4	1910.7
27	3/07/89	46.6	1396.8
28	3/14/89	45.7	130.1
29	3/30/89	45.7	1163.3
30	4/06/89	27.7	648.2
31	4/12/89	36.9	359.4
32	4/19/89	37.5	9.8
33	4/26/89	38.7	89.8
34	5/04/89	39.3	71.7
35	5/11/89	40.8	138.5
36	*5/18/89	11.6	1386.1

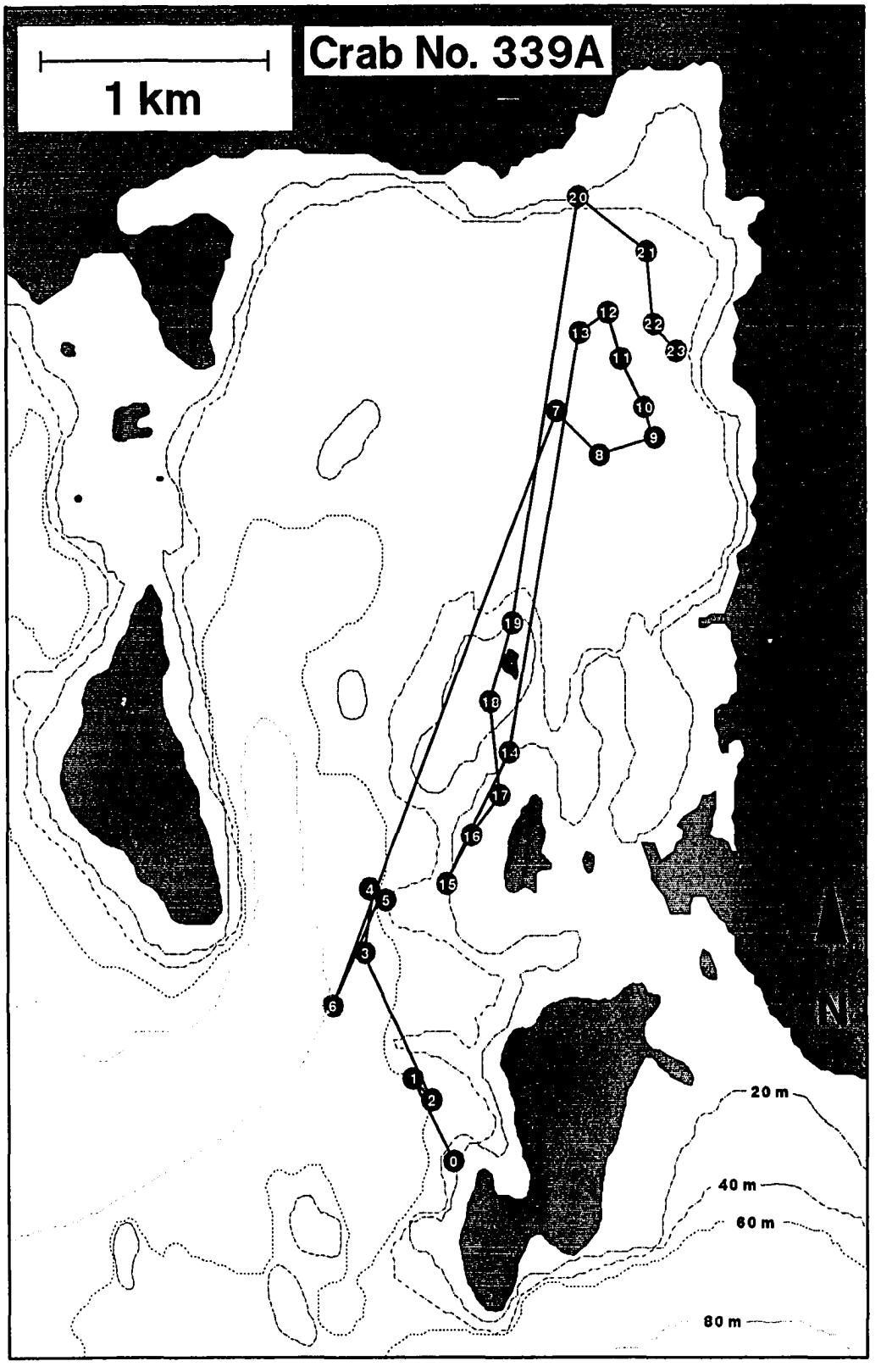
* The crab was retrieved by divers and molted in the laboratory on 5/20/89.

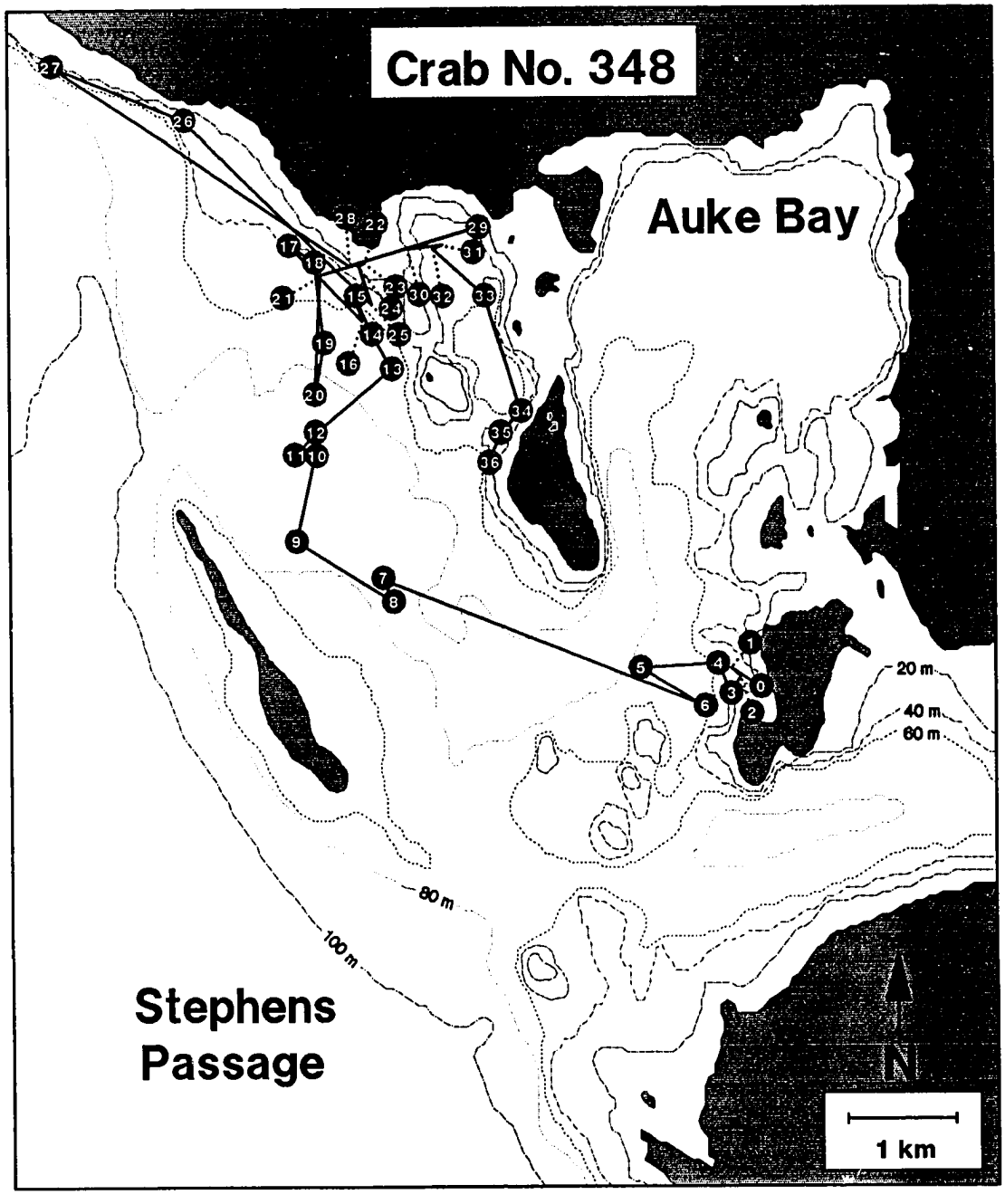
Appendices 23-44. Study area at Auke Bay, Alaska, showing the detailed movements of 22 female red king crabs fitted with ultrasonic transmitters. Numbered circles refer to weekly positions (sequence no.). The actual dates for each position may be cross-referenced in Appendices 1-22, respectively. Consecutive positions are connected by straight solid lines. Dashed lines indicate the shortest presumptive trek when the straight-line trek intersected land or shoals. Dotted lines show the true location of each weekly position when consecutive positions were indistinguishable. Depth contours are in meters.

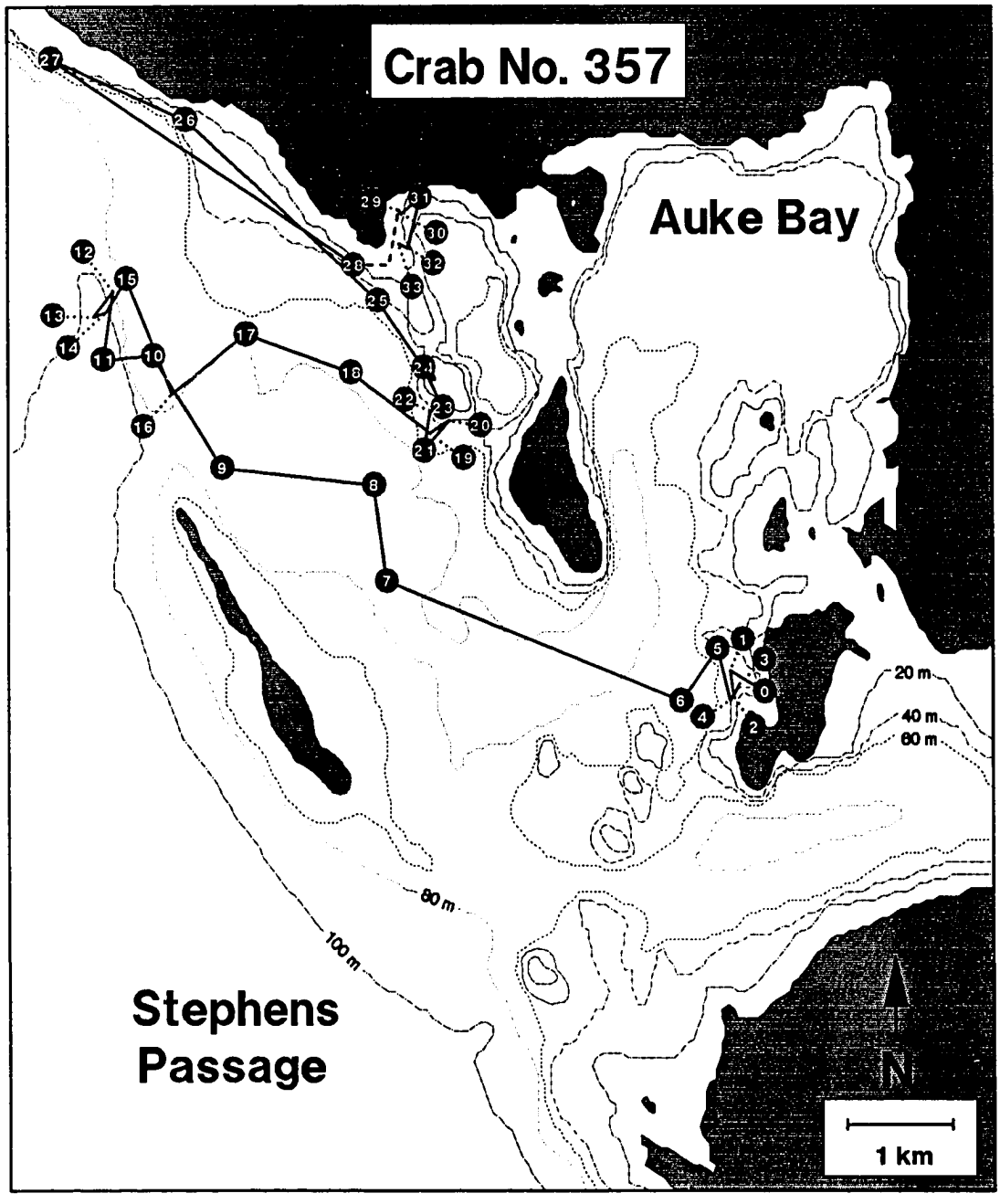


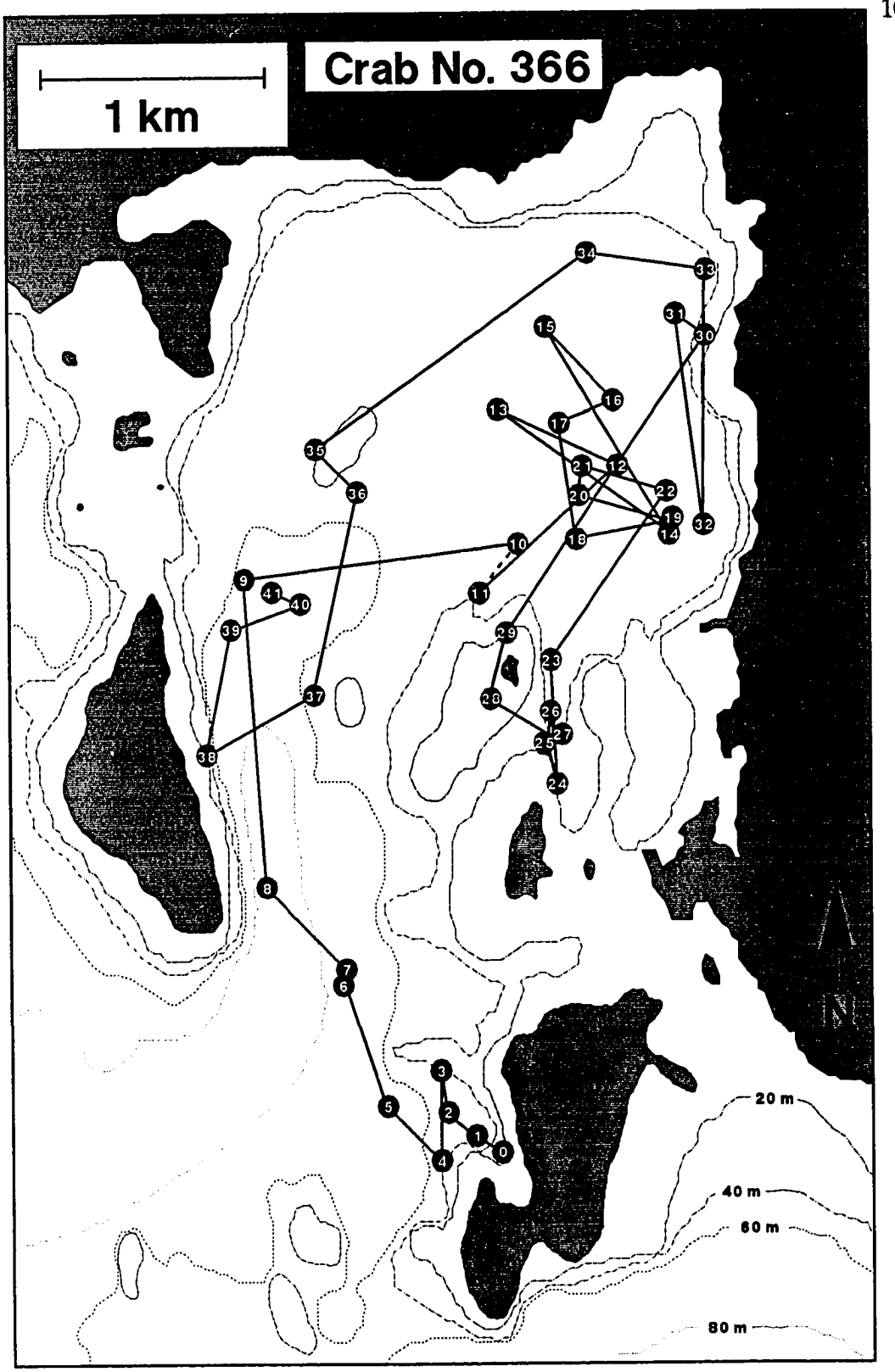


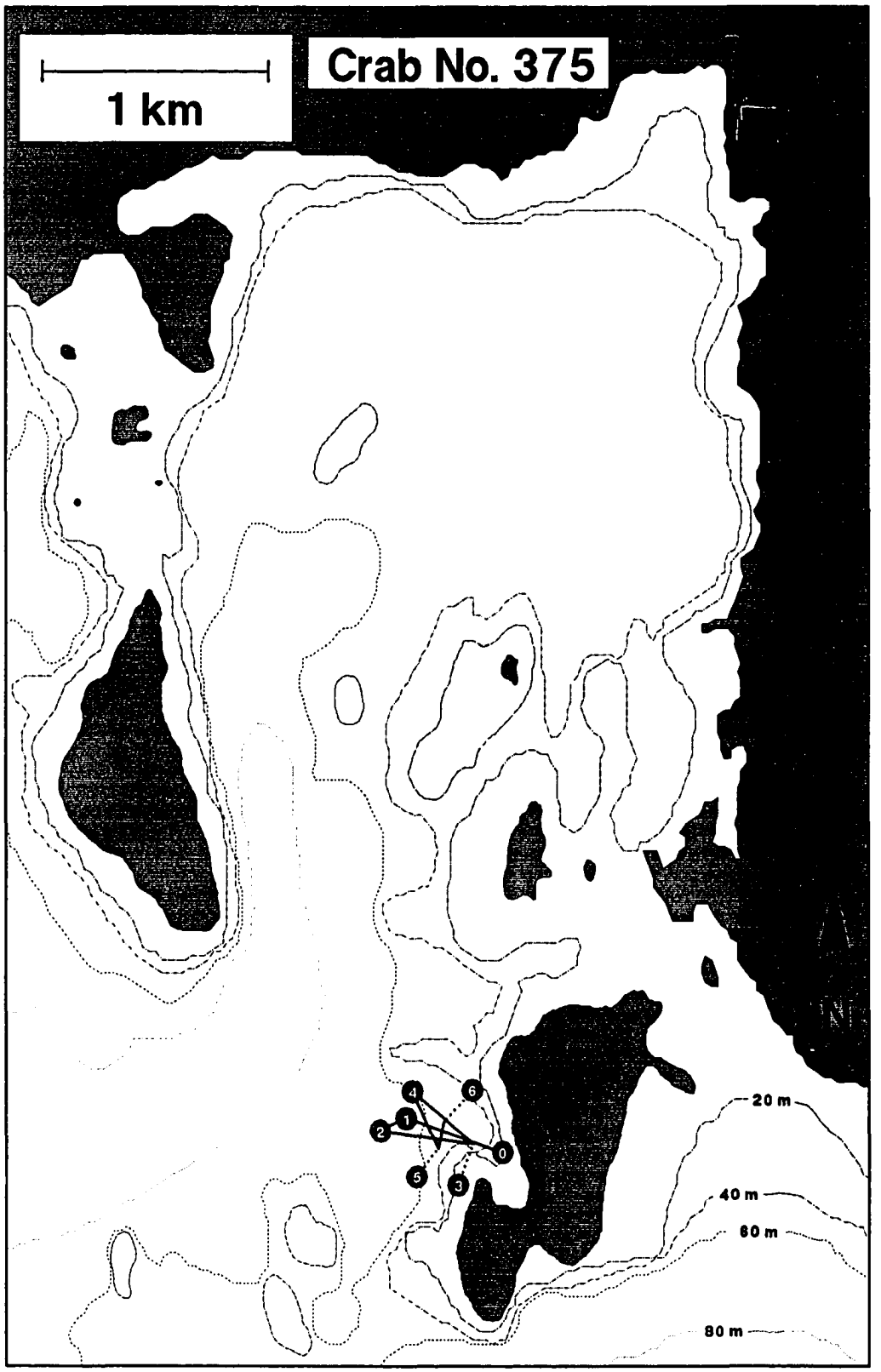


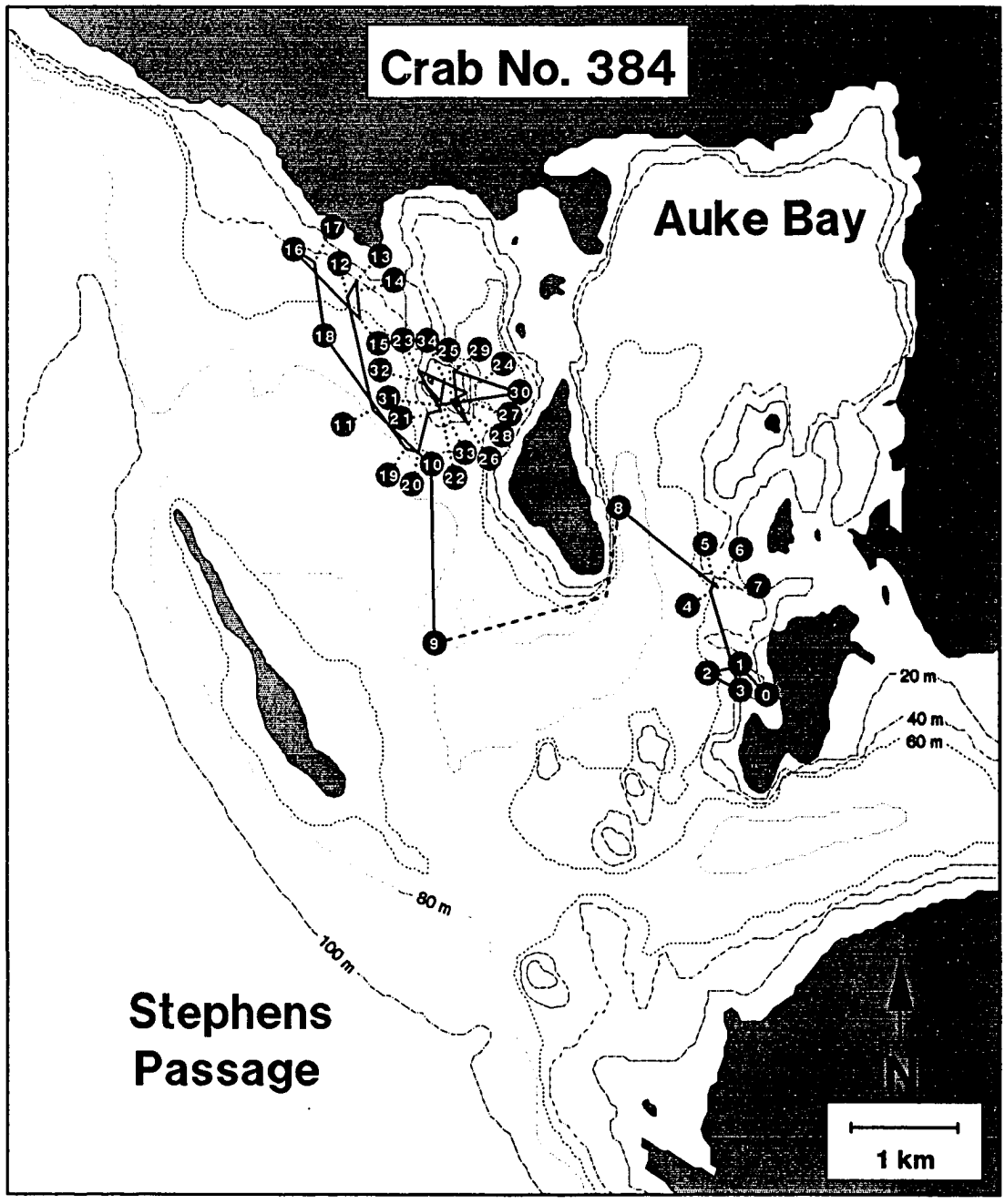


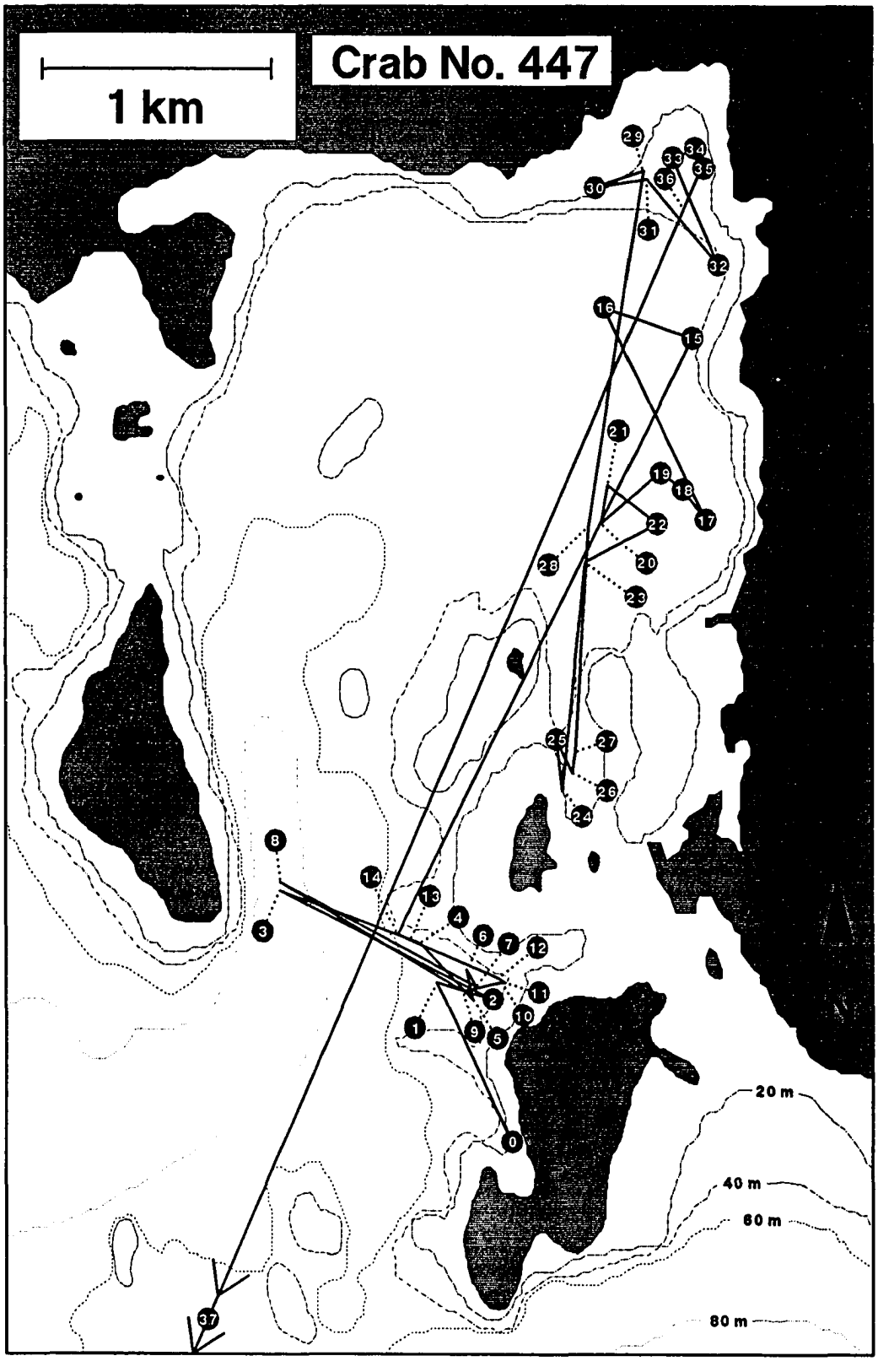


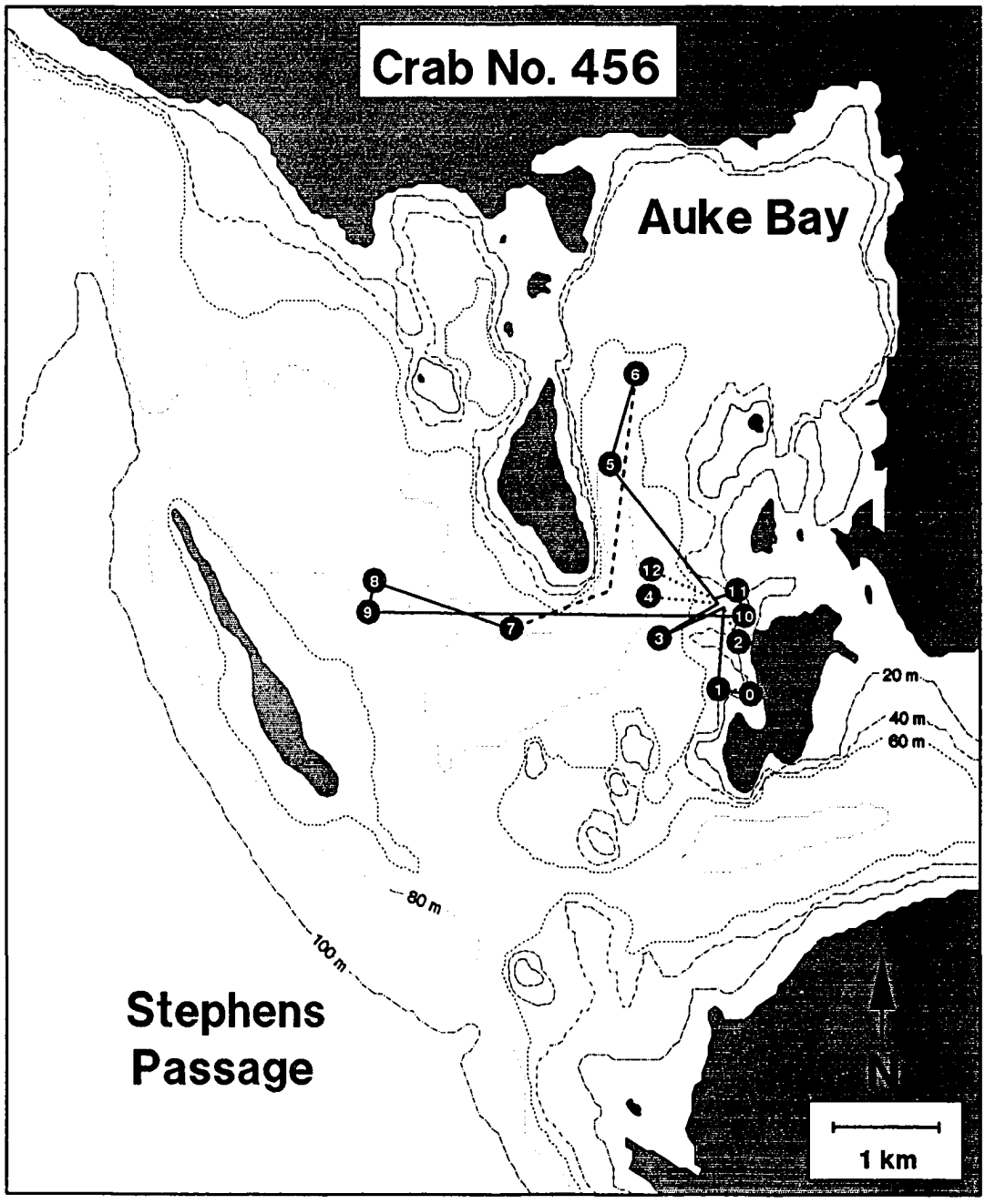


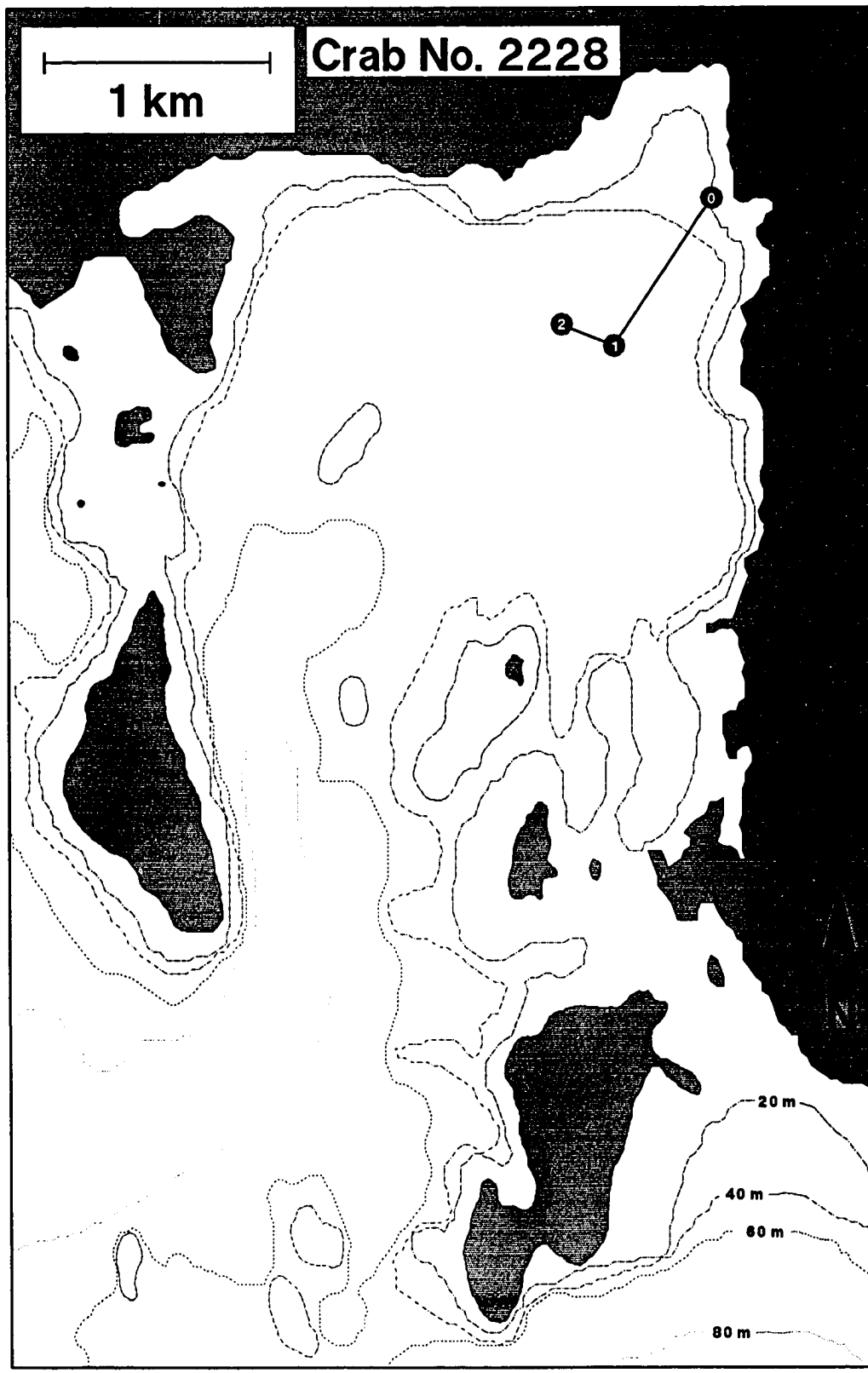


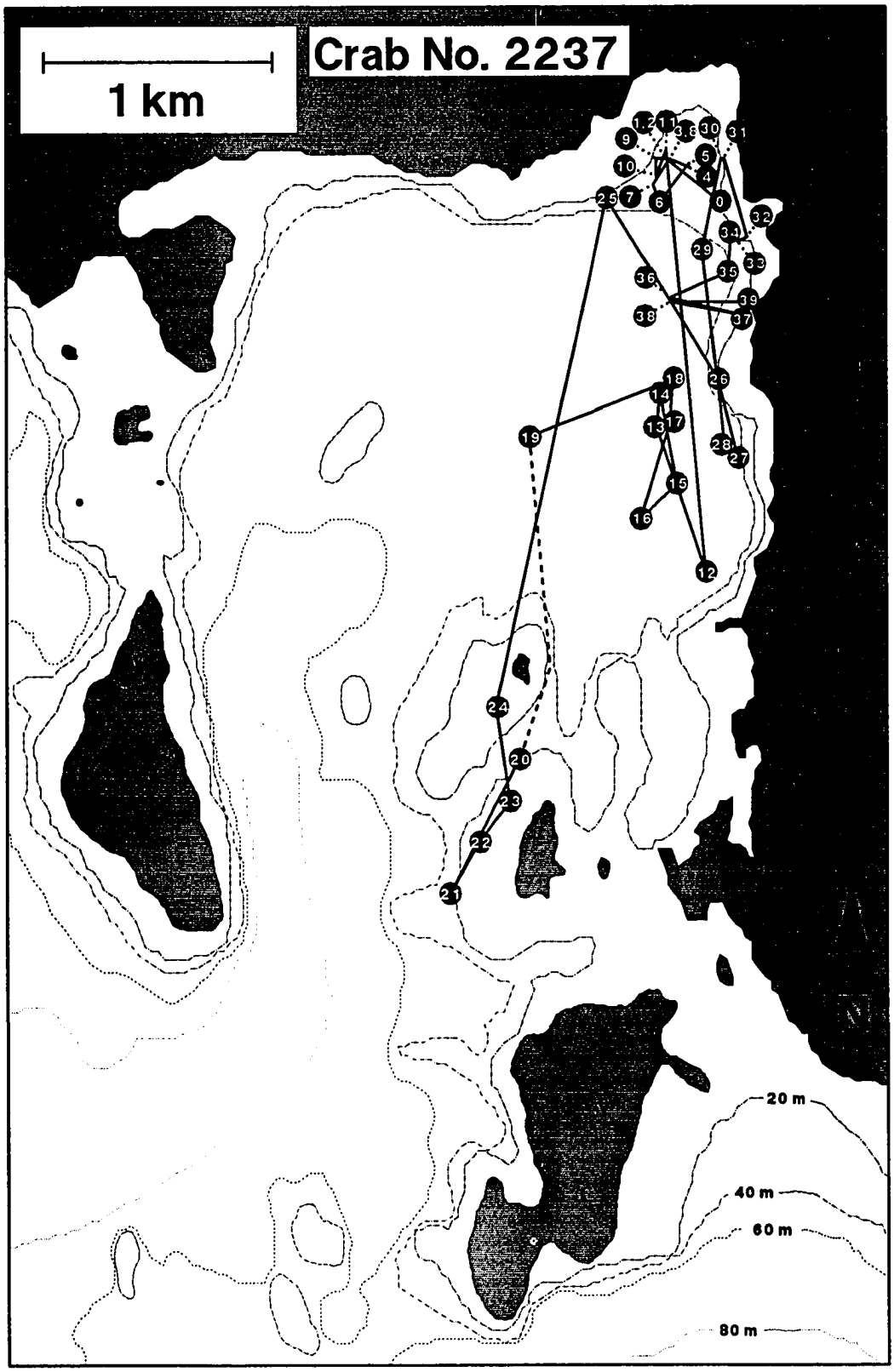


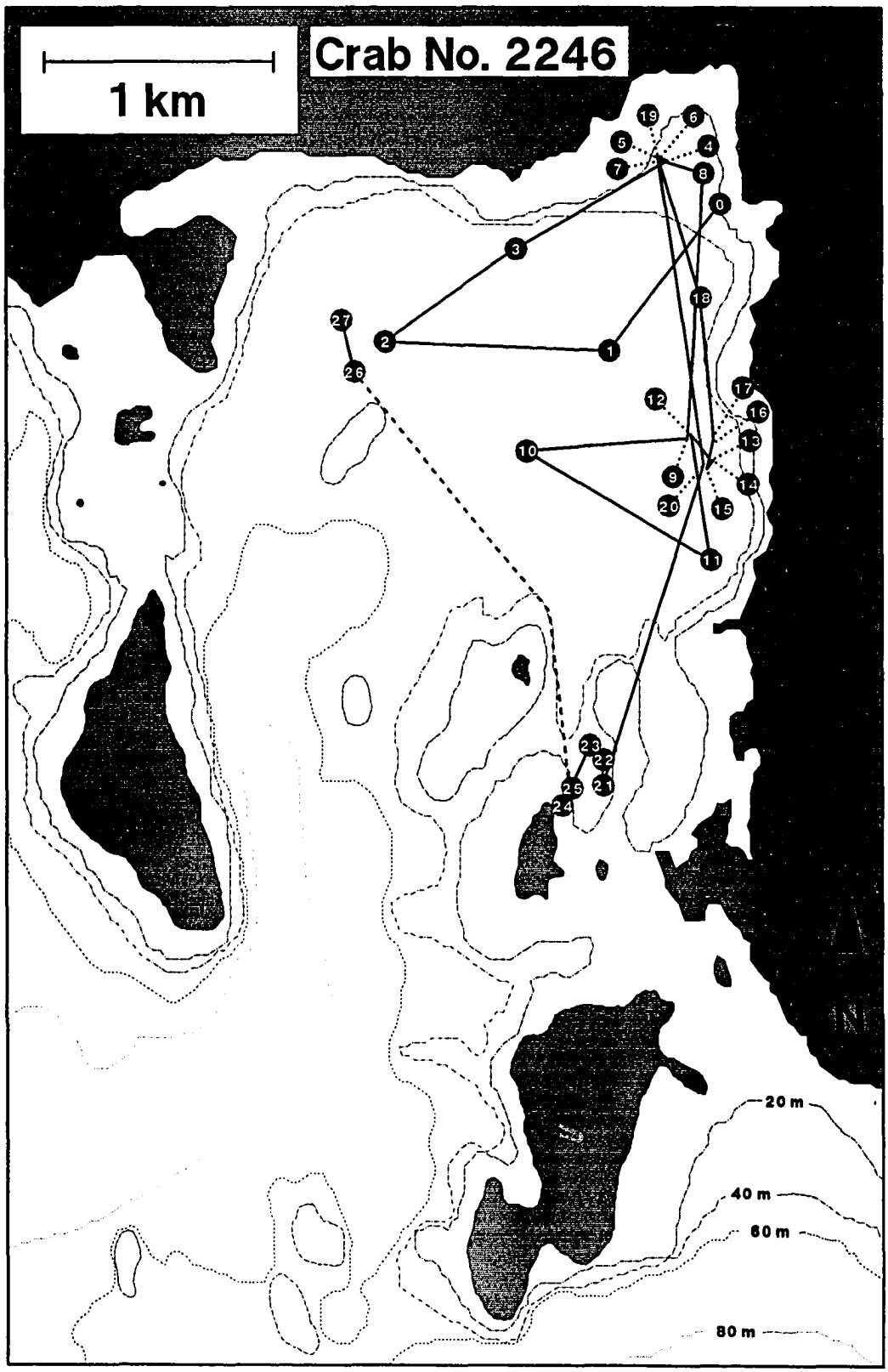


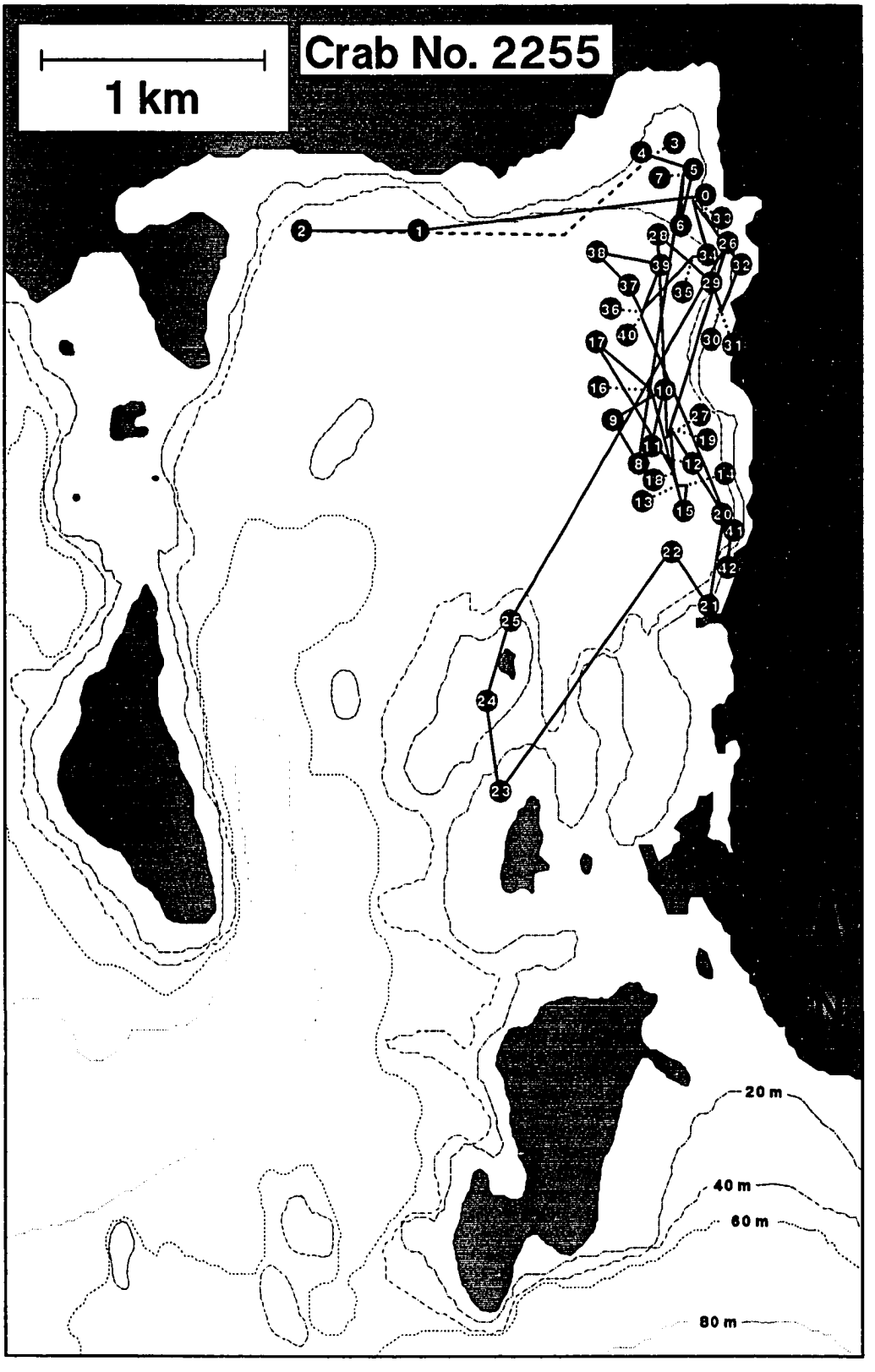


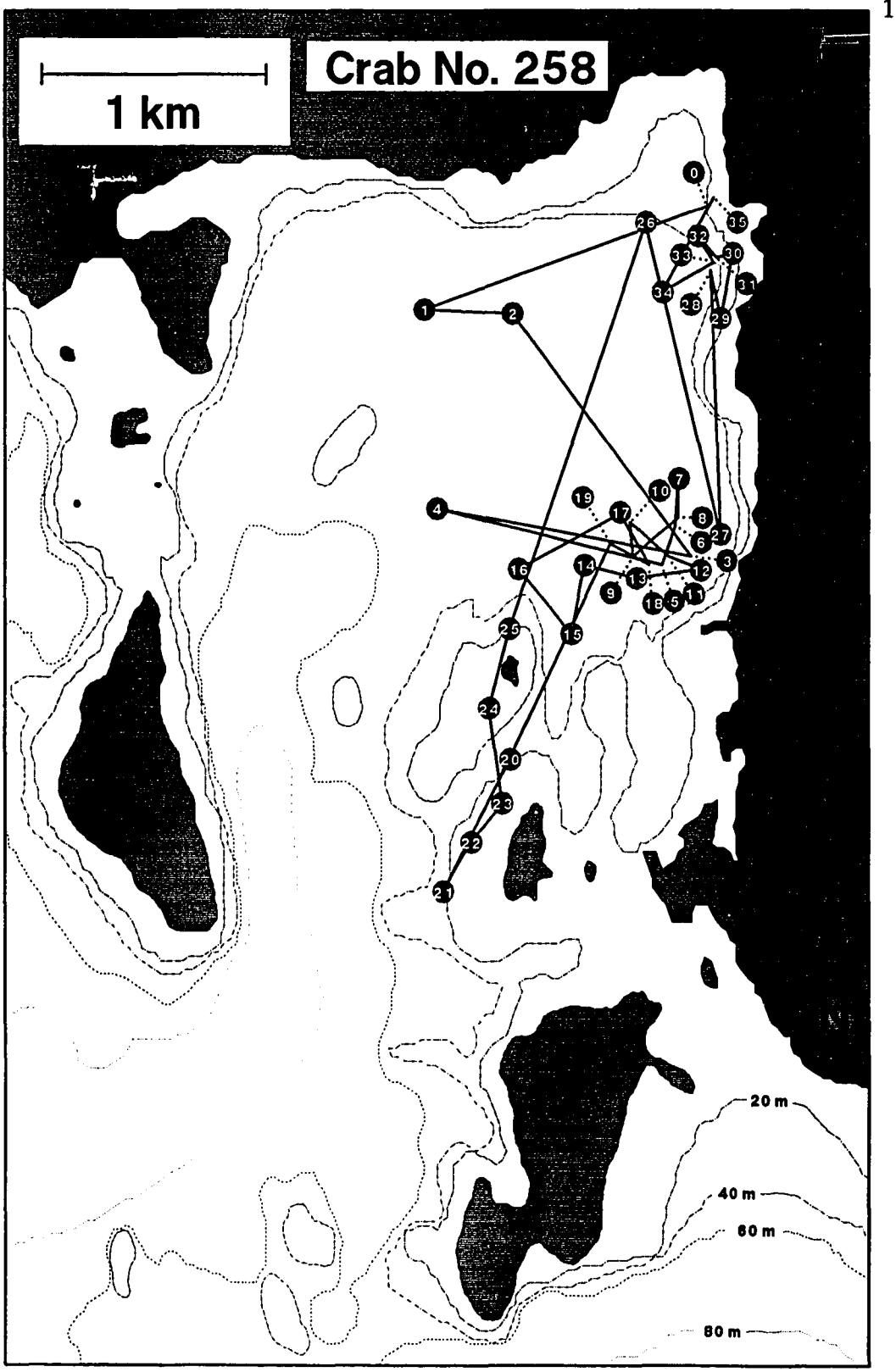


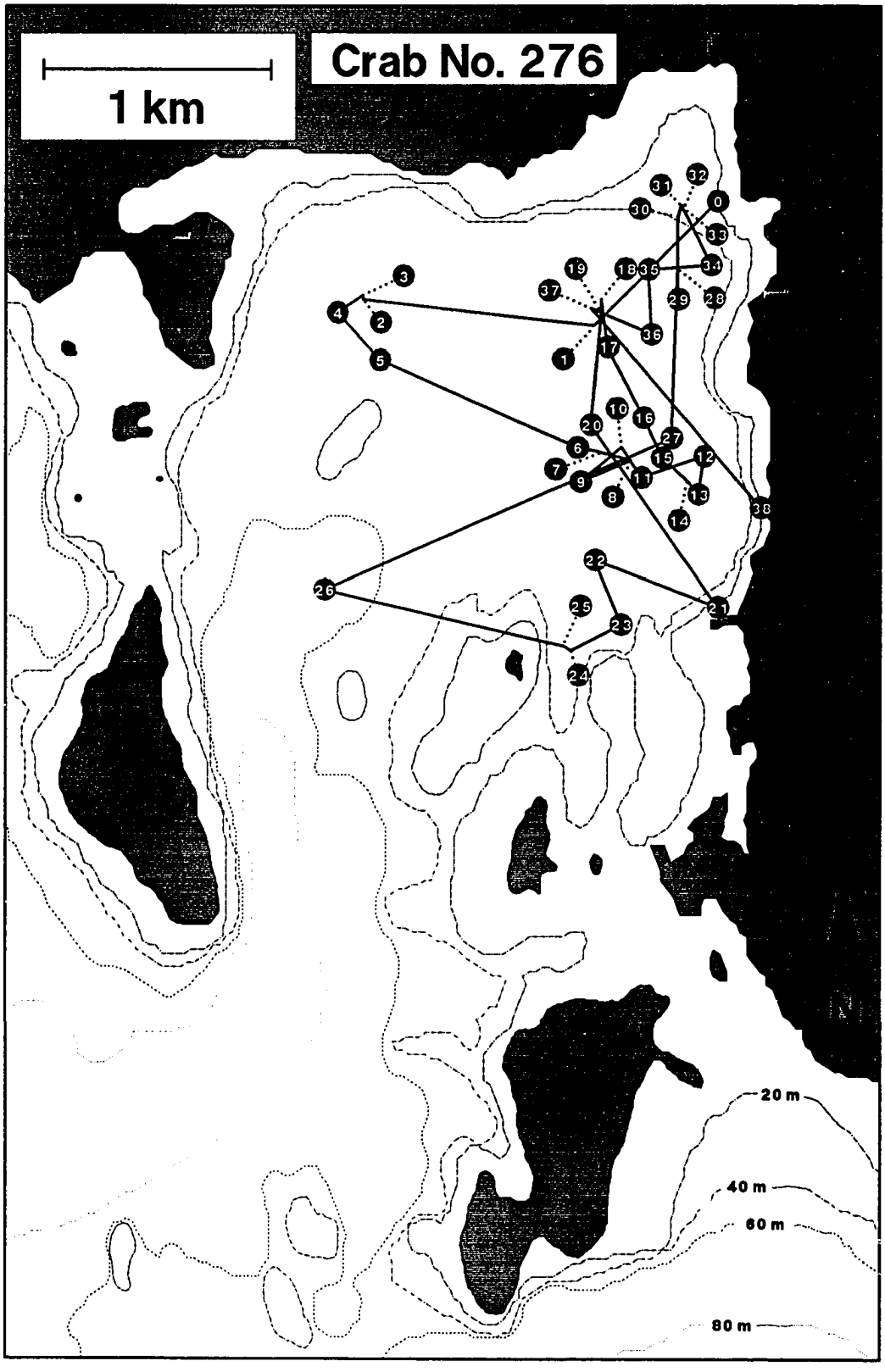


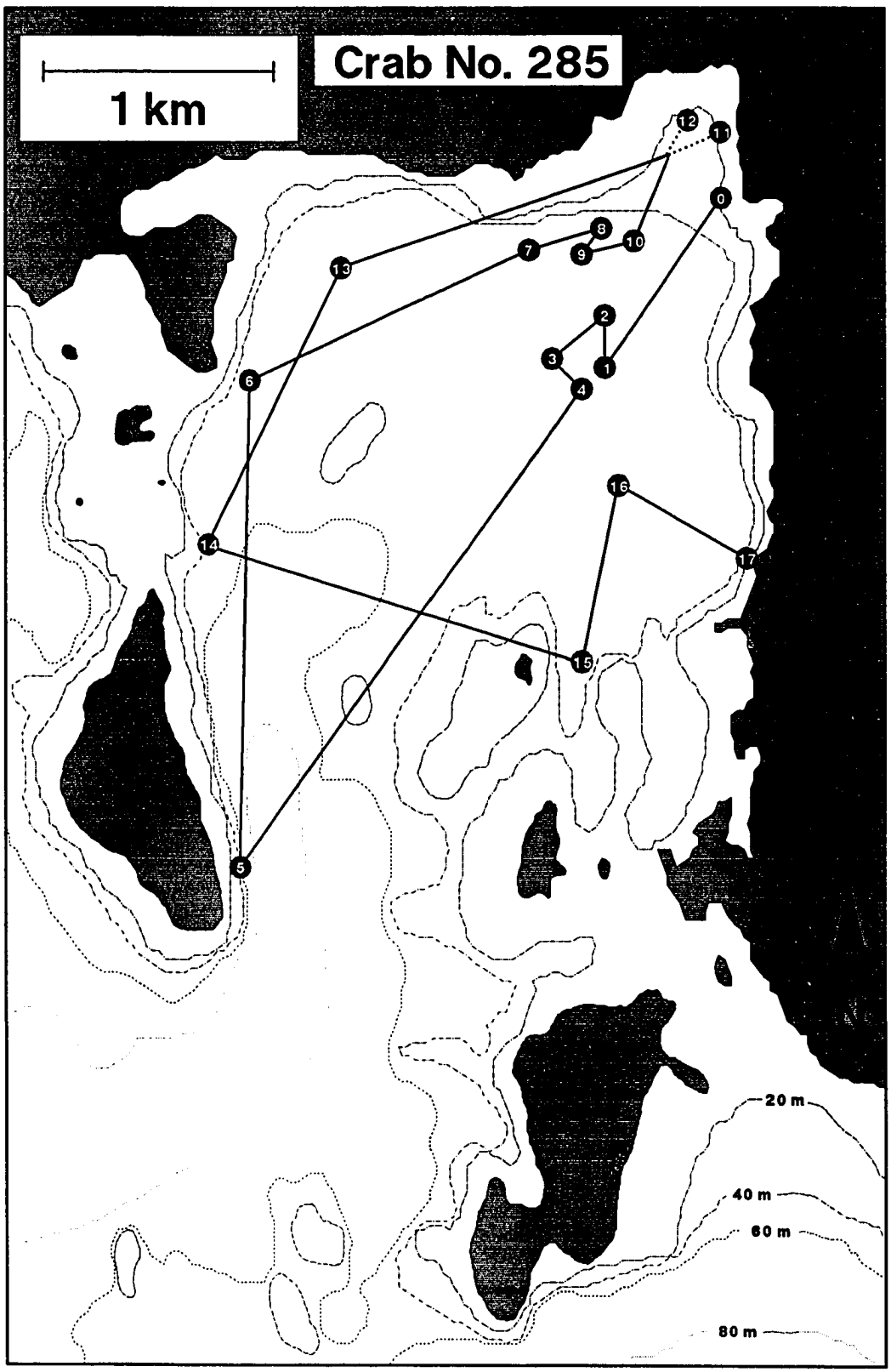


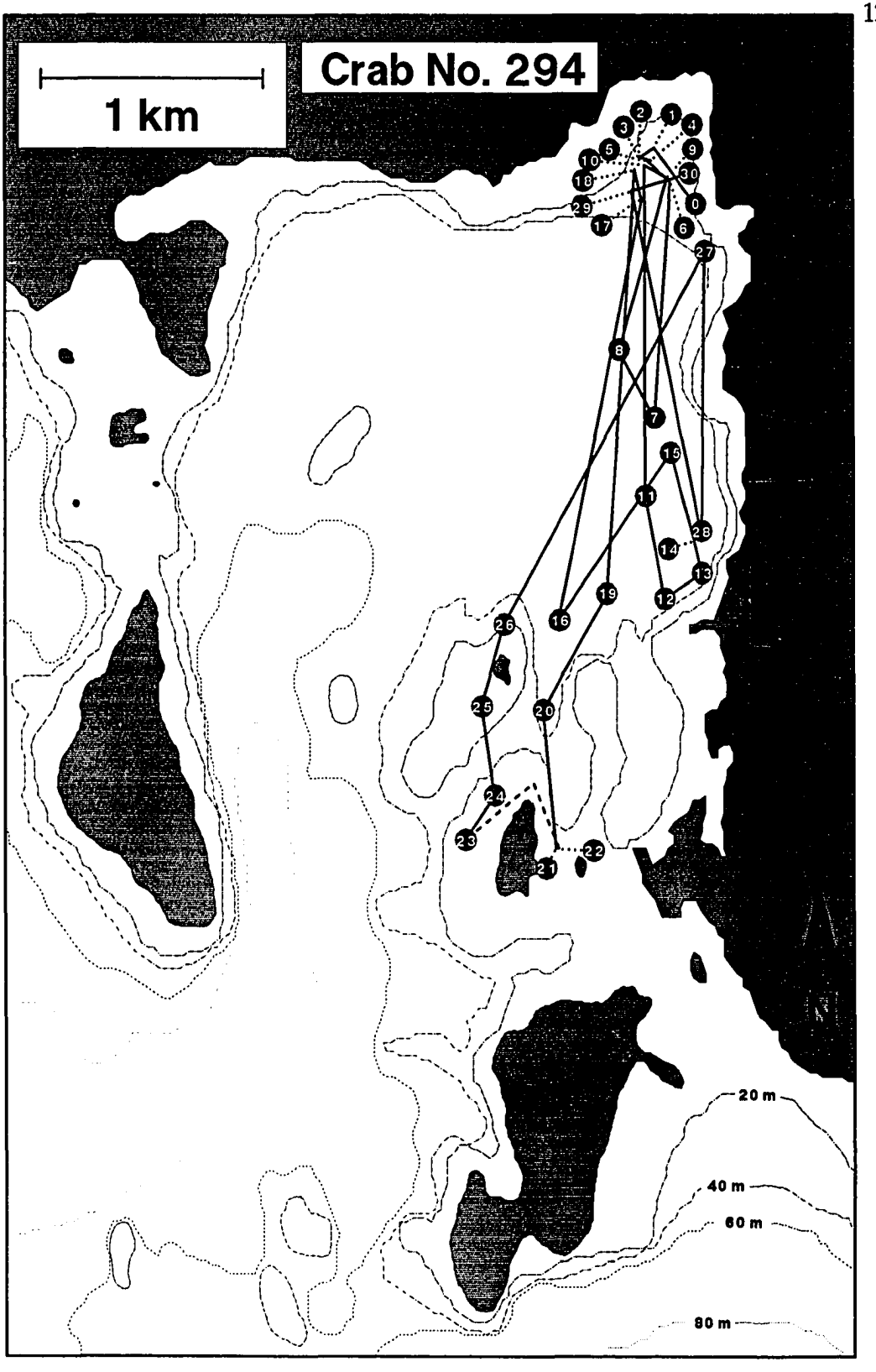


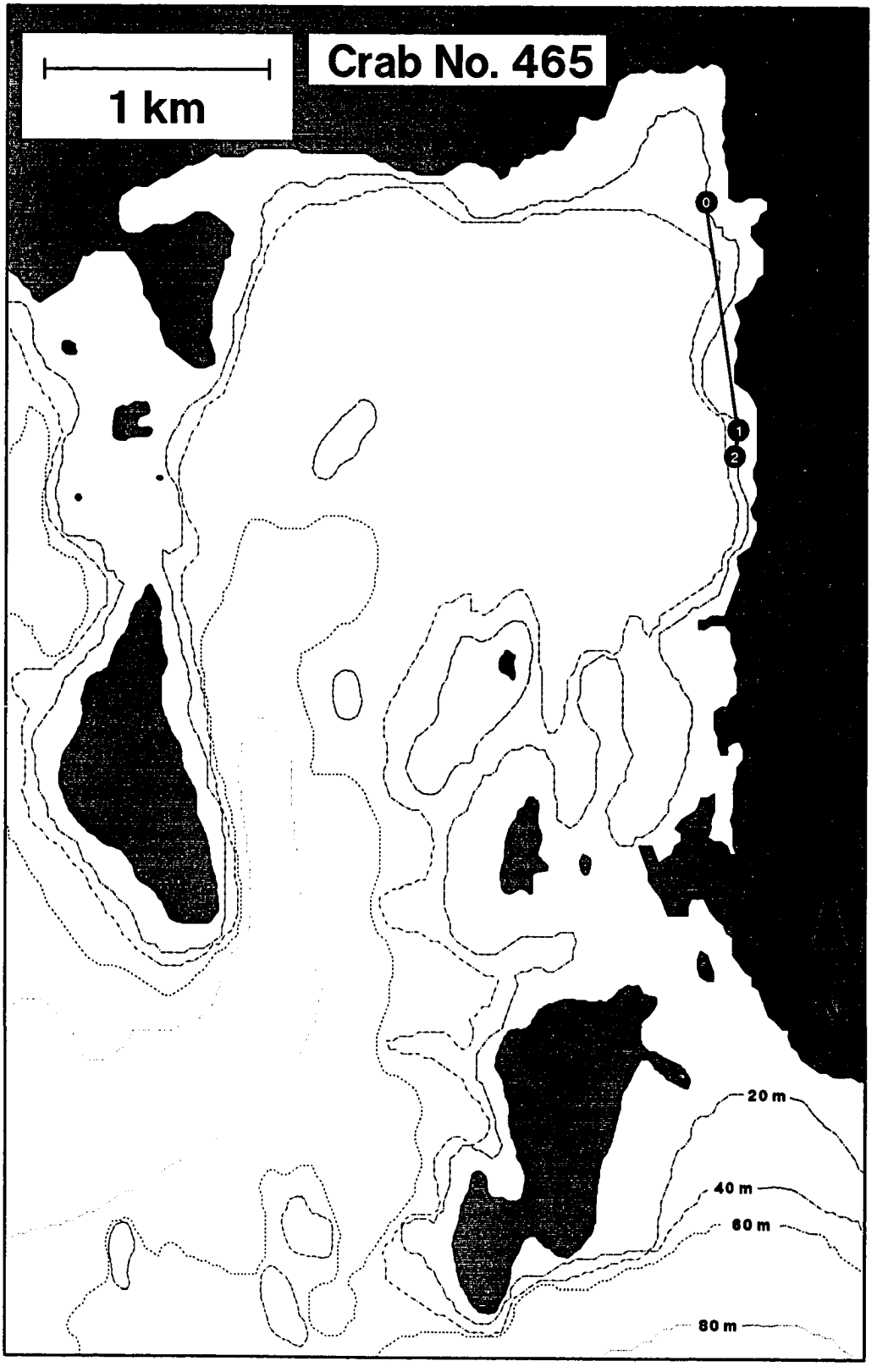


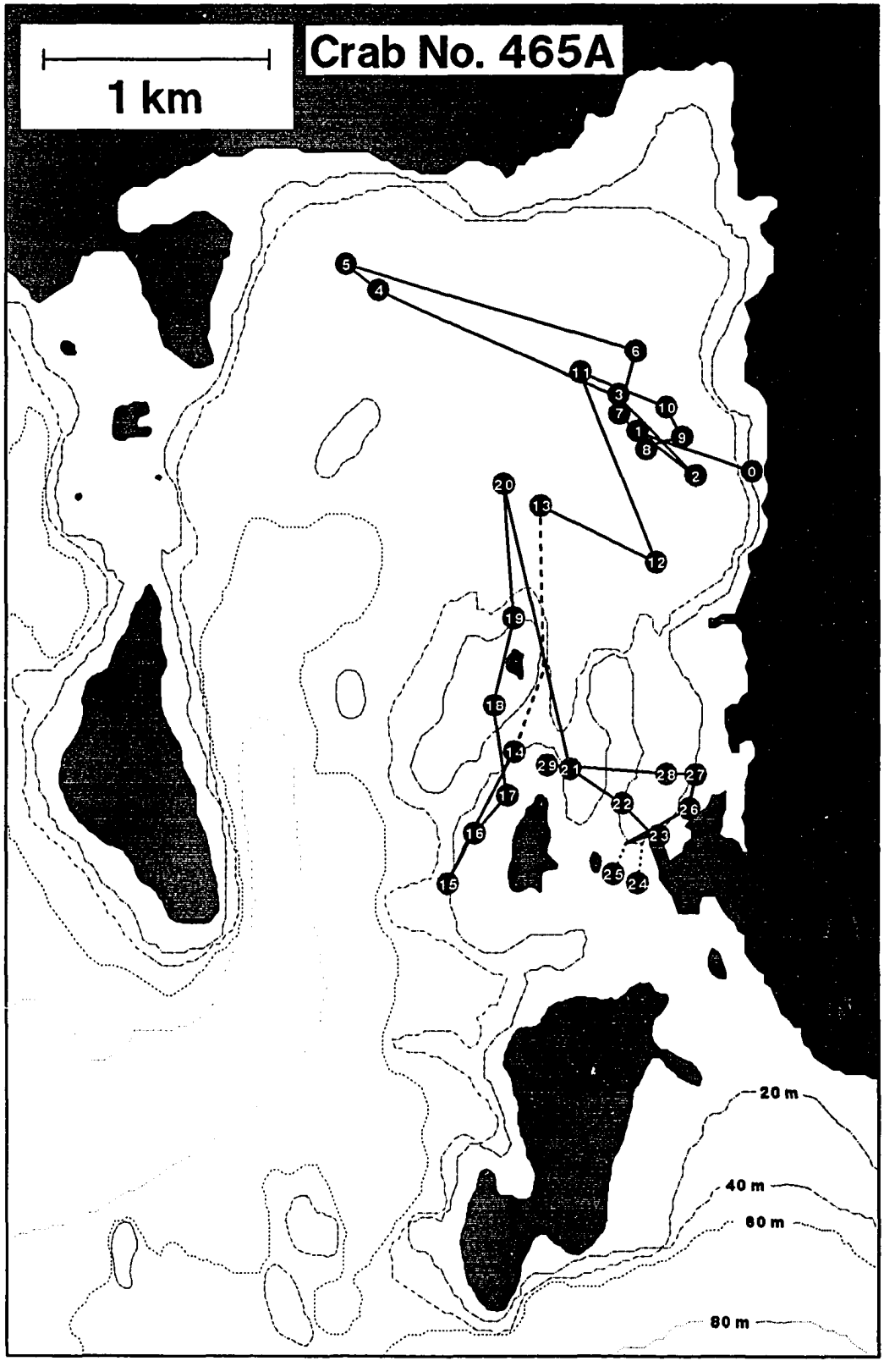


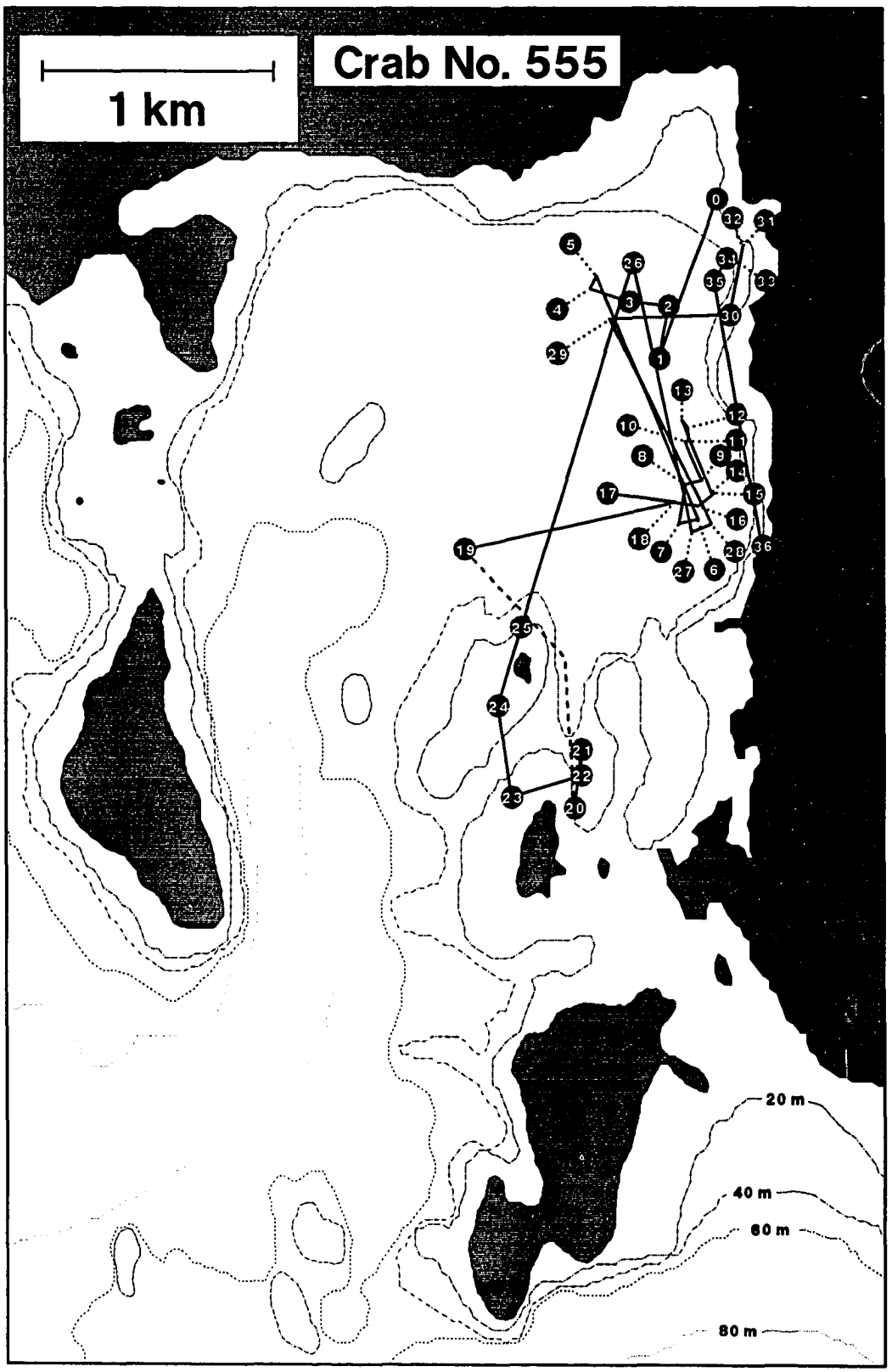












Appendix 45. Tag number, total distance moved after release, and total number of days tracked for 22 female red king crabs fitted with ultrasonic transmitters.

Tag No.	Total Distance (m)	Total Days Tracked
Primiparous Females		
249	24,538	355
267	22,066	337
339	414	41
339A	14,587	241
348	26,464	348
357	25,533	328
366	25,557	361
375	2,131	55
384	17,240	338
447	27,265	355
456	13,315	105
Multiparous Females		
2228	1,211	21
2237	18,066	355
2246	16,729	264
2255	22,431	361
258	20,693	347
276	17,290	355
285	17,287	145
294	21,172	300
465	1,318	18
465A	15,474	289
555	16,825	349

Literature Cited

Able, K. P. 1991. Common themes and variations in animal orientation systems. – American Zoologist 31: 157-167.

Allen, J.A. 1966. The rhythm and population dynamics of Decapod crustacea. – Oceanography and Marine Biology Annual Review 4: 247-265.

Atkinson, R. J. A. and A. J. Parsons. 1973. Seasonal patterns of migration and locomotor rhythmicity in populations of *Carcinus*. – Netherlands Journal of Sea Research 7: 81-93.

Autodesk, Inc.. 1988. Autocad Release 10. Oakland, CA., 467 pp.

Baggerman, B. 1960. Factors in the diadromous migration of fish. – Symposia of the Zoological Society of London 1: 33-60.

Bainbridge, R. 1961. Migration. – *In:* T. H. Waterman, ed., The Physiology of Crustacea. Vol. 2, pp. 431-463. Academic Press, New York.

Banse, K. 1964. On the vertical distribution of zooplankton in the sea. – Progress in Oceanography 2: 53-125.

Bennett, D. B., and C. G. Brown. 1983. Crab (*Cancer pagurus*) migrations in the English Channel. – Journal of the Marine Biological Association of the United Kingdom 63: 371-398.

Berrill, M. 1975. Gregarious behavior of juveniles of the spiny lobster, *Panulirus argus* (Crustacea: Decapoda). – Bulletin of Marine Science 25(4): 515-512.

Blau, F. 1986. Recent declines of red king crab *Paralithodes camtschatica* populations and reproductive conditions around the Kodiak Archipelago, Alaska. – *In:* G. S. Jamieson and N. Bourne, eds., North Pacific workshop on stock assessment and management of invertebrates. Canadian Special Publication of Fisheries and Aquatic Sciences 92: 360-369.

Bollens, S. M., and B. W. Frost. 1989. Predator-induced diel vertical migration in a planktonic copepod. – Journal of Plankton Research 11(5): 1047-1065.

Bright, D. B., F. E. Durham, and J. W. Knudsen. 1960. King crab investigations of Cook Inlet, Alaska. – Allan Hancock Foundation, Department of Biology, University of Southern California, Los Angeles, California. Pp. 1-180.

Bright, D. 1967. Life histories of the king crab, *Paralithodes camtschatica*, and the Tanner crab, *Chionoecetes bairdi* (sic), in Cook Inlet, Alaska. – Ph.D. thesis, University of Southern California, Los Angeles, California. Pp. 1-265.

Brown, J. L., and G. H. Orians. 1970. Spacing patterns in mobile animals. – *In:* R. F. Johnston, ed., Annual review of ecology and systematics. Vol. 1, pp. 239-262. Annual Reviews Inc., Palo Alto, California.

Bruce, E. B., D. R. McLain, and B. L. Wing. 1977. Annual physical and chemical oceanographic cycles of Auke Bay, Southeastern Alaska. – NOAA Technical Report NMFS SSRF-712. Pp. 1-11.

Butler, T. H. 1960. Maturity and breeding of the Pacific edible crab, *Cancer magister* Dana. – Journal of the Fisheries Research Board of Canada 17: 641-

646.

Campbell, A. 1990. Aggregations of berried lobsters (*Homarus americanus*) in shallow waters off Grand Manan, Eastern Canada. – Canadian Journal of Fisheries and Aquatic Sciences 47: 520-523.

Campbell, A. and A. B. Stasko. 1985. Movements of tagged American lobsters, *Homarus americanus*, off southwestern Nova Scotia. – Canadian Journal of Fisheries and Aquatic Sciences 42: 229-237.

Carlisle, D. B. 1957. On the hormonal inhibition of molting in decapod crustaceans. II. The terminal anecdysis in crabs. – Journal of the Marine Biological Association of the United Kingdom 36: 291-307.

Carls, M. G. and C. E. O'Clair. 1990. Influence of cold air exposures on ovigerous red king crabs (*Paralithodes camtschatica*) and Tanner crabs (*Chionoecetes bairdi*) and their offspring. – *In:* Proceedings of the International Symposium on King and Tanner Crabs, Anchorage, Alaska, November 28-30, 1989. Pp. 329-343. University of Alaska, Alaska Sea Grant College Program Report No. 90-04.

Chapman, C. J., A. D. F. Johnstone, and A. L. Rice. 1975. The behavior and ecology of the Norway lobster, *Nephrops norvegicus* (L.). – *In:* H. Barnes, ed., Proceedings of the Ninth European Marine Biology Symposium. Pp. 59-74. Aberdeen University Press, Oban, Scotland.

Creutzberg, F. 1975. Orientation in space: Animals (8.1) invertebrates. – *In:* O.

Kinne, ed., Marine Ecology - A Comprehensive, Integrated Treatise on Life in Oceans and Coastal Waters. Volume II. Physiological Mechanisms. Part 2. John Wiley and Sons, New York, New York. Pp. 555-565.

Cushing, D. H. 1951. The vertical migration of planktonic Crustacea. – Biological Review 26: 158-192.

DeGoursey, R. E., and L. L. Stewart. 1985. Spider crab podding behavior and mass molting. – Underwater Naturalist 15: 12-16.

Dew, C. B. 1990. Behavioral ecology of podding red king crab, *Paralithodes camtschatica*. – Canadian Journal of Fisheries and Aquatic Sciences 47: 1944-1958.

Diamond, N. and D. G. Hankin. 1985. Movements of adult female Dungeness crabs (*Cancer magister*) in northern California based on tag recoveries. – Canadian Journal of Fisheries and Aquatic Sciences 42: 919-926.

Dingle, H. 1962. The occurrence and ecological significance of color responses in some marine Crustacea. – American Naturalist 96: 151-160.

Dingle, H. and S. A. Gauthreaux, Jr. 1991. Introduction to the symposium: the maturing of migration. – American Zoologist 31: 153-155.

Dorgelo, J. 1976. Salt tolerance in Crustacea and the influence of temperature upon it. – Biological Reviews of the Cambridge Philosophical Society 51: 255-290.

Durham, F. E. 1960. Observation of aggregations of young king crabs

(Paralithodes camtschatica) Tilesius, in Kachemak Bay, Alaska. – *In:* "Science in Alaska". Proceedings of the Ninth Alaska Science Conference, College, Alaska, 2-5 September 1958. American Association for the Advancement of Science, Alaska Division, College, Alaska. 173pp.

Edgington, E. S. 1987. Randomization tests, second edition. – Marcel Dekker, Inc., New York, New York. Pp. 1-341.

Enright, J. T. 1978. Migration and homing of marine invertebrates: a potpourri of strategies. – *In:* K. Schmidt-Koenig and W. T. Keeton, eds., Animal migration, navigation, and homing. Springer-Verlag, Berlin. Pp. 440-446.

Enright, J. T. and W. M. Hamner. 1967. Vertical diurnal migration and endogenous rhythmicity. – Science 154: 532-533.

Forward, R. B. Jr. 1976. Light and diurnal vertical migration: photobehavior and photophysiology of plankton. – *In:* K. Smith, ed., Photochemical and photobiological review, Vol. 1. Plenum Press, New York, New York. Pp. 157-209.

Goddard, S. M., and R. B. Forward Jr. 1989. The use of celestial cues in the offshore escape response of the shrimp, *Palaemonetes vulgaris*. – Marine Behavior and Physiology 16: 11-18.

Gotshall, D. W. 1978. Northern California Dungeness crab, *Cancer magister*, movements as shown by tagging. – California Fish and Game 64: 234-254.

Gray, G. W. 1963. Growth of mature female king crab *Paralithodes camtschatica*

(Tilesius). – Alaska Department of Fish and Game, Division of Biological Research, Informational Leaflet 26, Juneau. Pp. 1-4.

Hamilton, W. D. 1971. Selection of selfish and altruistic behavior in some extreme models. – *In:* J. F. Eisenberg and W. S. Dillon, eds., Smithsonian Annual III. Man and beast: comparative social behavior. Pp. 58-91. Smithsonian Institution Press, Washington D. C.

Hamner, W. M., M. Smyth, and E. D. Mulford Jr. 1968. Orientation of the sand-beach isopod *Tylos punctatus*. – Animal Behavior 16: 405-409.

Hanauer, E. 1988. Spider crab orgy. – Skindiver 37 (6): 28-29.

Harden-Jones, F. R. 1980. The nekton: production and migration patterns. – *In:* R. S. K. Barnes and K. H. Mann, eds., Fundamentals of Aquatic Ecosystems. Blackwell Scientific Publications, Oxford. Pp. 119-142.

Hardy, A. C., and W. N. Paton. 1947. Experiments on the vertical migration of plankton animals. – Journal of the Marine Biological Association of the United Kingdom 26: 467-523.

Hartsuyker, L. 1966. Daily tidal migrations of the shrimp, *Crangon crangon* L. – Netherlands Journal of Sea Research 3 (1): 52-67.

Hayes, M. L., and D. T. Montgomery. 1962. Movements of tagged king crabs from offshore releases, Shumagin Islands area, 1957-62. – Manuscript Report MR 62-9. Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska: Pp. 1-10.

Hayes, M. L., and D. T. Montgomery. 1963. Movements of king crabs tagged and released in Shumagin Island area 1957-62. – Special Scientific Reports, United States Fish and Wildlife Service - Fisheries 458: Pp. 1-7.

Haynes, E. B. 1974. Distribution and relative abundance of larvae of king crab, *Paralithodes camtschatica*, in the south-eastern Bering Sea, 1969-70. – Fishery Bulletin [National Oceanic and Atmospheric Administration] 72(3): 804-812.

Herring, P. J., and H. S. J. Roe. 1988. The photoecology of pelagic oceanic decapods. – Symposia of the Zoological Society of London 59: 263-290.

Herrnkind, W. F. 1968. Adaptive, visually-directed orientation in *Uca pugilator*. – American Zoologist 8: 585-598.

Herrnkind, W. F. 1980. Spiny lobsters: patterns of movement. – *In:* J. S. Cobb, and B. F. Morris, eds., The Biology and Management of Lobsters, Vol. I: Physiology and Behavior. Pp. 349-407. Academic Press, New York.

Herrnkind, W. F. and R. McLean. 1971. Field studies of homing, mass emigration and orientation in the spiny lobster, *Panulirus argus*. – Annals of the New York Academy of Science 188: 359-377.

Herrnkind, W. F., and P. Kanciruk. 1978. Mass migration of spiny lobster, *Panulirus argus* (Crustacea: Palinuridae): Synopsis and orientation. – *In:* K. Schmidt-Koenig and W. T. Keeton, eds., Animal migration, navigation, and homing. Pp. 430-439. Springer-Verlag, Berlin.

Hill, B. J. 1978. Activity, track and speed of movement of the crab *Scylla serrata*

in an estuary. – Marine Biology 47: 135-141.

Hsu, C. C. 1987. Spatial and temporal distribution patterns of female red king crabs in the southeastern Bering Sea. – Ph.D. dissertation, School of Fisheries, University of Washington, Seattle, Washington. Pp. 1- 300.

Ireland, L. C. and R. B. Barlow. 1978. Tracking normal and blindfolded *Limulus* in the ocean by means of acoustic telemetry. – The Biological Bulletin 155: 445-446.

Jernakoff, P. 1987. Foraging patterns of juvenile western rock lobsters *Panulirus cygnus* George. – Journal of Experimental Marine Biology and Ecology 113: 125-144.

Jewett, S. C., and H. M. Feder. 1982. Food and feeding habits of the king crab *Paralithodes camtschatica* near Kodiak Island, Alaska. – Marine Biology 66: 243-250.

Jewett, S. C., and G. C. Powell. 1981. Nearshore movement of king crab. – Alaska Seas and Coasts 9(3): 6-8.

Jewett, S. C., and C. P. Onuf. 1988. Habitat suitability index models: red king crab. – Biological Reports [U.S. Fish and Wildlife Service, National Wetlands Research Center, Slidell, Louisiana] 82(10.153). Pp. 1-34.

Kanciruk, P., and W. F. Herrnkind. 1976. Autumnal reproduction of spiny lobsters, *P. argus*, at Bimini, Bahamas. – Bulletin of Marine Science 26: 417-432.

Kanciruk, P., and W. F. Herrnkind. 1978. Mass migration of spiny lobster,

Panulirus argus (Crustacea: Palinuridae): Population dynamics, environmental correlates and triggering stimuli. – Bulletin of Marine Science 28: 601-623.

Koch, H. 1989. The effect of tidal inundation on the activity and behavior of the supralittoral talitrid amphipod *Traskorchestia traskiana* (Stimpson, 1857). – Crustaceana 57 (3): 295-303.

Kurata, H. 1959. Studies on the larva and post-larva of *Paralithodes camtschatica*. I. Rearing of the larvae, with special reference to the food of the zoea. – Bulletin of the Hokkaido Regional Fisheries Research Laboratory 20: 76-83.

Lund, W. A., and R. C. Lockwood, Jr. 1970. Sonic tag for large decapod crustaceans. – Journal of the Fisheries Research Board of Canada 27: 1147-1151.

Magurran, A. E. 1990. The adaptive significance of schooling as an anti-predator defence in fish. – Annales de Zoologici Fennici 27: 51-66.

Marukawa, H. 1933. Biological and fishery research on Japanese king crab *Paralithodes camtschatica* (Tilesius). – Journal of the Imperial Fisheries Experimental Station 4(37): 1-152.

McLaren, I. A. 1963. Effects of temperature on growth of zooplankton and the adaptive value of vertical migration. – Journal of the Fisheries Research Board of Canada 20: 685-727.

McMurray, G., A. Vogel, P. Fishman, D. Armstrong, and S. Jewett. 1984.

Distribution of larval and juvenile red king crabs (*Paralithodes camtschatica*) in Bristol Bay. – *In:* Final Report to Outer Continental Shelf Environmental Assessment Program (OCSEAP), February, 1984. NOAA, Anchorage. 210 p.

Mitchell, C. T., C. H. Turner, and A. R. Strachan. 1969. Observations on the biology of the California spiny lobster, *Panulirus interruptus* (Randall). – California Fish and Game 53: 121-131.

Nakanishi, T. 1985. The effects of the environment on the survival rate, growth and respiration of eggs, larvae and post-larvae of king crab (*Paralithodes camtschatica*). – *In:* Proceedings of the International King Crab Symposium, Anchorage, Alaska, January 22-24, 1985. Pp. 167-185. University of Alaska, Alaska Sea Grant Report No. 85-12.

Nishimoto, R. T., and W. F. Herrnkind. 1982. Orientation of the blue crab *Callinectes sapidus* Rathbun: role of celestial cues. – Marine Behaviour and Physiology 9: 1-11.

O'Clair, C. E., R. P. Stone, and J. L. Freese. 1990. Movements and habitat use of Dungeness crabs and the Glacier Bay fishery. – *In:* Milner, A. M. and J. D. Wood, eds., Proceedings of the Second Glacier Bay Science Symposium: September 19-22, 1988. Gustavus, Alaska. U.S. Department of the Interior, National Park Service, Alaska Regional Office, Anchorage, Alaska. pp. 74-77.

Otto, R. S. 1986. Management and assessment of eastern Bering Sea king crab stocks. – *In:* G. S. Jamieson and N. Bourne, eds., North Pacific workshop on

stock assessment and management of invertebrates. Canadian Special Publication of Fisheries and Aquatic Sciences 92: 83-106.

Pardi, L., and A. Ercolini. 1986. Zonal recovery mechanisms in talitrid crustaceans. – Bollettino di Zoologia 53: 139-160.

Paul, A. J., and J. M. Paul. 1980. The effect of early starvation on later feeding success of king crab zoeae *Paralithodes camtschatica.* – Journal of Experimental Marine Biology and Ecology 44: 247-251.

Phillips, B. F., L. M. Joll, and D. C. Ramm. 1984. An electromagnetic tracking system for studying the movements of rock (spiny) lobsters. – Journal of Experimental Marine Biology and Ecology 79: 9-18.

Poole, R. W. 1974. An introduction to quantitative ecology. – McGraw-Hill, Inc., New York, New York. Pp. 1-532.

Powell, G. C. 1964. Fishing mortality and movements of adult male king crabs, *Paralithodes camtschatica* (Tilesius), released seaward from Kodiak Island, Alaska. – Transactions of the American Fisheries Society 93(3): 295-300.

Powell, G. C. 1965. Tagged king crab recaptured six years after release in the North Pacific. – Transactions of the American Fisheries Society 94(1): 95.

Powell, G. C. 1972. King crab, *Paralithodes camtschatica* (Tilesius) pods. – Skin Diver 21(10): 20-21.

Powell, G. C. 1974. Gregarious king crabs. – Sea Frontiers 20(4): 206-211.

Powell, G. C., and R. B. Nickerson. 1965a. Reproduction of king crabs

Paralithodes camtschatica (Tilesius). – Journal of the Fisheries Research Board of Canada 22: 101-111.

Powell, G. C., and R. B. Nickerson. 1965b. Aggregations among juvenile king crabs (*Paralithodes camtschatica*, Tilesius) Kodiak, Alaska. – Animal Behavior 13(2-3): 374-380.

Powell, G. C., and R. E. Reynolds. 1965. Movements of tagged king crabs *Paralithodes camtschatica* (Tilesius) in the Kodiak Island - Lower Cook Inlet Region of Alaska, 1954 - 1963. – Alaska Department of Fish and Game, Informational Leaflet 55: 1-10.

Powell, G. C., B. Shafford, and M. Jones. 1972. Reproductive biology of young adult king crabs *Paralithodes camtschatica* (Tilesius) at Kodiak, Alaska. – Proceedings of the National Shellfisheries Association 63: 77-87.

Rebach, S. 1974. Burying behavior in relation to substrate and temperature in the hermit crab, *Pagurus longicarpus*. – Ecology 55: 195-198.

Rice, A. L. 1964. Observations on the effects of changes of hydrostatic pressure on the behavior of some marine animals. – Journal of the Marine Biological Association of the United Kingdom 44: 163-175.

Rodin, V. E. 1970. Some data on the distribution of king crab *Paralithodes camtschatica* in the southeastern Bering Sea. – Soviet Fisheries Investigations in the north-eastern part of the Pacific Ocean, Part V. Pacific Science Research Institute of Fisheries & Oceanography (TINRO) 72: 140-158.

Rose, M. 1925. Contribution à l'étude de la biologie du plankton: le probléme des migrations verticales journaliéres. – Archives de Zoologie Experimentale et Generale 64: 387-542.

Rumyantsev, L. E. 1945. The migration of crab along the southern part of the west coast of Kamchatica. – Izvestiia Tikhookeans-kovo Nauchno-Issledovatelskovo Instituta Rybnogo Knoziaistvai Okeanografii 19: 55-70.

Rusanowski, P. C., L. A. Gardner, and S. C. Jewett. 1987. Nome Offshore Placer Project: Annual Report - 1986. – Northern Technical Services, Inc., Anchorage Alaska. Pp. 1-380.

Saila, S. B., and J. M. Flowers. 1968. Movements and behavior of berried female lobsters displaced from offshore areas to Narragansett Bay, Rhode Island. – Journal Du Conseil 31(3): 342-351.

Seeb, L., and J. E. Seeb. 1987. Gene expression and variation among populations of red king crab (*Paralithodes camtschatica*). – Final Report to Alaska Department of Fish and Game. Department of Biology and Science, University of Idaho, Moscow, Idaho. Pp. 1-48.

Shirley, S. M., and T. C. Shirley. 1988a. Behavior of red king crab larvae: phototaxis, geotaxis and rheotaxis. – Marine Behaviour and Physiology 13: 369-388.

Shirley, S. M., and T. C. Shirley. 1989. Interannual variability in density, timing and survival of Alaskan red king crab *Paralithodes camtschatica* larvae. – Marine

Ecology Progress Series 54: 51-59.

Shirley, T. C., and S. M. Shirley. 1988b. Variables affecting hatching time of Alaskan red king crab. – American Zoologist 28(4): 63A.

Shirley, T. C., and S. M. Shirley. 1990. Planktonic survival of red king crab larvae in a subarctic ecosystem, 1985-1989. – *In:* D. A. Ziemann, and K. W. Fulton-Bennett, eds., APPRISE – Interannual Variability and Fisheries Recruitment. Pp. 263-285. The Oceanic Institute, Honolulu, Hawaii.

Shirley, T. C., S. M. Shirley, and S. Korn. 1990. Incubation period, molting and growth of female red king crabs: effects of temperature. – *In:* Proceedings of the International Symposium on King and Tanner Crabs, Anchorage, Alaska, November 28-30, 1989. Pp. 51-63. University of Alaska, Alaska Sea Grant College Program Report No. 90-04.

Simpson, R. R., and H. H. Shippen. 1968. Movement and recovery of tagged king crabs in the eastern Bering Sea, 1955-63. – International North Pacific Fisheries Commission, Bulletin 24: 111-123.

Sinclair, D. F. 1985. On tests of spatial randomness using mean nearest neighbor distance. – Ecology 66(3): 1084-1085.

Sloan, N. A. 1985. Life history characteristics of fjord-dwelling golden king crabs *Lithodes aequispina*. – Marine Ecology Progress Series 22: 219-228.

Smith, B. D., and G. S. Jamieson. 1991. Movement, spatial distribution, and mortality of male and female Dungeness crab *Cancer magister* near Tofino,

British Columbia. – Fishery Bulletin 89(1): 137-148.

Smith, F. E., and E. R. Baylor. 1953. Color responses in the Cladocera and their ecological significance. – American Naturalist 57: 49.

Somerton, D. A. 1985. The disjunct distribution of blue king crab, *Paralithodes platypus* in Alaska: some hypotheses. – *In:* Proceedings of the International King Crab Symposium, Anchorage, Alaska, January 22-24, 1985. Pp. 13-21. University of Alaska, Alaska Sea Grant Report No. 85-12.

Starr, M., J. H. Hamilton, and J. Therriault. 1990. Direct coupling of marine invertebrate spawning with phytoplankton blooms. – Science 247: 1071-1074.

Ševčić, Z. 1971. Laboratory observations on the aggregations of the spiny spider crab (*Maja squinado* Herbst). – Animal Behavior 19: 18-25.

Stinson, J. E. 1975. The effect of ocean currents, bottom temperatures, and other biological considerations in regard to the location and abundance of mature southeastern Bering Sea king crab (*Paralithodes camtschatica*). – University of Washington, Fisheries Research Institute, Manuscript Report 499: Pp. 1-20.

Sundberg, K and D. Clausen. 1977. Post-larval king crab (*Paralithodes camtschatica*) distribution and abundance in Kachemak Bay, Lower Cook Inlet, Alaska, 1976. – *In:* Trasky, L.L., L. B. Flagg, and D. C. Burbank, eds., Environmental Studies of Kachemak Bay and Lower Cook Inlet, Vol. 5. Alaska Department of Fish and Game, Anchorage. Pp. 1-36.

U. S. Department of Commerce. 1988. West Coast of North and South America

including the Hawaiian Islands. – *In:* Tide Tables 1989, Pp. 193-202. National Ocean Service, NOAA.

Vinogradov, L. G. 1945. The annual life and migration cycle of crabs from the northern part of the West Kamchatka Shelf. – *In:* Data on the biology fishery and processing of the Kamchatka crab. [TINRO] 19: 3-54.

Vinogradov, L. G. 1969. The mechanism of reproduction of the stock of Kamchatka crab (*Paralithodes camtschatica*) in the Okhotsk Sea off the western coast of Kamtchatka. – Trudy Vsesoyuznogo Nauchno-Issledovatel'skogo Instituta Morskogo Rybnogo Khozyaistva i Okeanografii [VNIRO] 65: 337-344.

Wallace, M. M., L. J. Pervit, and A. R. Hvatum. 1949. Contribution to the biology of the king crab (*P. camtschatica*). – U.S. Department of the Interior, Fish and Wildlife Service Leaflet 34: 1-50.

Warner, W. 1976. Winter "drudging" lifts crabs from their beds. – Smithsonian 6(11): 82-89.

Warwick, R. M., C. L. George, and J. R. Davies. 1978. Annual macrofauna production in a *Venus* Community. – Estuarine and Coastal Marine Science 7: 215-241.

Weber, D. D. 1965. Growth of the immature king crab *Paralithodes camtschatica* (Tilesius). – Masters Thesis, University of Washington, Seattle. Pp. 1-100.

Wing, B. L. 1976. Ecology of *Parathemisto libellula* and *P. pacifica* (Amphipoda: Hyperiidea) in Alaskan coastal waters. – Northwest Fisheries Center Processed

Report, NOAA. Pp. 1-266.

Wolcott, T. G., and A. H. Hines. 1989. Ultrasonic biotelemetry of muscle activity from free-ranging marine animals: a new method for studying foraging by blue crabs (*Callinectes sapidus*). – Biological Bulletin 176: 50-56.

Wolcott, T. G., and A. H. Hines. 1990. Ultrasonic telemetry of small-scale movements and microhabitat selection by molting blue crabs (*Callinectes sapidus*). – Bulletin of Marine Science 46(1): 83-94.

Worton, B. J. 1987. A review of models of home range for animal movements. – Ecological Modelling 38: 277-298.

Yamamoto, T. 1961. Tagging experiments of the king crab in the west coast area of Kamchatka and with special reference to its migratory movement. – Bulletin of the Japanese Society of Scientific Fisheries 27(2): 128-136.

Ziemann, D. A., L. D. Conquest, K. W. Fulton-Bennett, and P. K. Bienfang. 1990. Interannual variability in the Auke Bay phytoplankton. – *In:* D. A. Ziemann, and K. W. Fulton-Bennett, eds., APPRISE – Interannual Variability and Fisheries Recruitment. Pp. 129-170. The Oceanic Institute, Honolulu, Hawaii.